

The Castniid Palm Borer, *Paysandisia archon* (BURMEISTER, 1880), in Europe: Comparative biology, pest status and possible control methods (Lepidoptera: Castniidae)

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Abstract: *Paysandisia archon* (BURMEISTER, 1880) is a Neotropical species of Castniidae recently introduced into Europe (from Argentina), where it has become a serious pest of palm trees. Since it was first reported in Catalonia (Spain) in March 2001, it has also been found in the Comunidad Valenciana and the Balearic Islands (Spain), several Departments in southeastern France, Italy (Sicily, Campania, Lazio, Marche) and even in Sussex (U.K.). Its life history and life cycle were not known in detail previously and are presented here, comparing them with those of other castniid pests, mainly *Telchin licus* (DRURY, 1773), *Castniomera atymnius* (DALMAN, 1824) and *Eupalamides cyparissias* (FABRICIUS, 1776). The egg of *P. archon* (usually 4.4–5.2 mm long) is fusiform, resembling a rice grain, bearing six to eight raised longitudinal ridges which have associated aeropyles along their length, with the micropyle at one end of the long axis; hatching occurs after 12–21 d, according to temperature. Larvae are endophagous; cannibalistic (even affecting prepupal larvae within their fully formed cocoons), mostly as a result of territoriality; undergo unusual lethargic periods and make “false cocoons”, most likely to confuse predators/parasitoids; generally go through nine instars (occasionally seven or eight), increasing dramatically in size (from ca. 0.7 cm to 9 cm), and in so doing have considerable destructive power. The total larval stage is quite long, ca. 10.5 months in larvae having a one-year cycle and ca. 18.5 months in larvae having an almost two-year cycle. Larvae can be found tunnelling in different parts of the palms, which largely depends on the larval size, although always on/near the top (crown) of the palm; they will normally not abandon their palm host until the adult stage is reached. The prepupal larval stage is long and complex, made up of two periods. The first occurs before making the cocoon and its length is very variable. The second occurs after the cocoon has been built and includes the time spent by the larva inside the cocoon before converting into pupa; this time is around 17 d in early spring although it can be shortened to only 9 d in early summer. The cocoons (av. length 5.8 cm) are stout with inner walls smoothly coated by a layer of silk and mucus and outer walls loosely covered by fragments of palm fibres which makes them very cryptic. Pupae formed in the second half of March took an average of 66 d to complete their metamorphosis to adults; those formed in the first half of April took 52 d; those formed in the first half of July took 43 d. The adult moths are day-flying insects. ♂♂ (which occur slightly less abundant than ♀♀, in the ratio of 1:1.19) are very territorial and fly in hot, sunny weather. Their flight is very powerful, rapid and darting (an estimation would be 20 m/s), being able to hover for a few seconds; the flight path is generally straight although right/left shifts are frequent and the moth can be seen balancing its body accordingly. They fly over and over rather small areas, returning to the same perching places. Their orientation skills are extraordinary; being capable of flying hundreds of meters, disappearing from human sight for several minutes and coming back exactly to the same

palm leaf they had taken off from. In the lab, ♀♀ lived an average of 14.1 d whereas ♂♂ lived 23.8 d, and both sexes do not appear to feed at all in this stage. Preliminary research indicates that sex recognition seems to be visual at first. ♀♀ simply move around within the appropriate habitat until they are spotted by a patrolling ♂, in much the same way as butterflies do. The fact that electroantennograms carried out using ♀ ovipositor (hexane) extracts, triggered a positive and significant response in ♂ antennae, seems to indicate that *P. archon* has at least a ♀-released short-range pheromone for conspecific sex recognition, while ♀-released long-range pheromone, i.e. that used by other heterocerans to attract conspecific ♂♂ at longer distances, might be absent in *P. archon* and replaced by visual attraction. Mating in the wild has been observed and described for the first time. ♀♀ lay eggs singly (through their long extensible ovipositor) in a very quick and inconspicuous manner; most eggs are found within the fibre webs closest to or within the palm crowns; they are not glued to the fibres, remaining loose within their thick layers (1–2 cm inside). Dissected virgin ♀♀, known to have laid no eggs, were found to have about 140 eggs. As for the life cycle, adults appear in the wild in mid-May and disappear in late September, with a peak during June and July; sightings of adults in May, August and September are much rarer. Live eggs are expected to be found from late May to mid-October. The larval stage is the longest and most complex of all *P. archon* stages. It is the only one that overwinters; during winter time, nearly all instars can be found within the palms in the wild, including prepupal ninth instar larvae. Most larvae will undergo a one-year cycle, although a second group will experience an almost two-year one. Live cocoons can be found from mid-March to mid-September. In summary, the *P. archon* life cycle in Catalonia comprises, from egg to egg, an average of 389 days (i.e. 12.8 months) in specimens undergoing a one-year cycle and an average of 673 days (i.e. 22.1 months) in specimens undergoing a two-year cycle. *P. archon* larvae seem to be specialized feeders on Arecaceae (palm trees) as all reported hostplants fall within this monocotyledonous family; however, within it, the larvae are unspecified feeders, given the variety of genera they attack. As to natural enemies, in Europe as well as in the Neotropics, there are no factual data as yet; however some empty eggs have been found in the wild in Catalonia strongly suggesting the attack by a hymenopterous egg parasitoid or an egg-predacious hemipteran. Very cold winter temperatures lasting for several consecutive days might increase mortality in the overwintering *archon* larval population sheltered in palm trees; notwithstanding that, this pest has proven to be well adapted to the Mediterranean climate. Symptoms of infestation by *P. archon* on palms are (1) presence of sawdust on the palm crown and/or palm trunk; (2) presence of perforated or nibbled leaves (non specific); (3) presence of gallery holes (axial and transversal) within the palm trunk (observable when the palm trunk is cut in slices); (4) abnormal development of axillary leaf buds; (5) deformation and

abnormal twisting of palm trunks; (6) abnormal drying up of the palms, especially the core leaves. As for possible measures of control, so far, only those using chemical insecticides have been tested (apart from pulling-up and burning the infested palms); good results were obtained by wetting the palm crown and palm trunk with contact and/or systemic organophosphorus insecticides (Chlorpyrifos, Acephate and Dimethoate); best results were obtained by using Chlorpyrifos 48 %, dose 200 ml/Hl, or Acephate 75 %, dose 150 g/Hl.

Key words: *Paysandisia archon*, Castniidae, palm pest, life history, life cycle, control, Giant Cane Borer, Banana Stalk Borer, Oil-Palm Borer

Der Castniiden-Palmenbohrer *Paysandisia archon* (BURMEISTER, 1880) in Europa: vergleichende Biologie, Schädlingsstatus und mögliche Bekämpfungsmethoden (Lepidoptera: Castniidae)

Zusammenfassung: *Paysandisia archon* (BURMEISTER, 1880) ist eine neotropische Castniidae-Art, die erst vor relativ kurzer Zeit nach Europa eingeführt wurde (aus Argentinien), wo sie sich als eine ernsthafte Gefahr für Palmen herausstellte. Nachdem sie in Katalonien (NO-Spanien) im März 2001 zuerst nachgewiesen wurde, konnte sie auch im Bereich Valencia und auf den Balearischen Inseln (Spanien), in verschiedenen südostfranzösischen Départements, in Italien (Sizilien, Campania, Lazio, Marche) und sogar in Sussex (England) gefunden werden. Biologie und Lebenszyklus waren bisher nicht vollständig bekannt und werden hier ausführlich dargestellt. Es wird mit anderen Schadarten aus der Familie Castniidae verglichen, insbesondere *Telchinlicus* (DRURY, 1773), *Castniomera atymnius* (DALMAN, 1824) und *Eupalamides cyparissias* (FABRICIUS, 1776). Das Ei von *P. archon* (4,4–5,2 mm lang) erinnert in der Form an ein Reiskorn; es hat 6–8 Längsrippen mit daran entlang angeordneten Aeropylonen und an einem Pol die Mikropyle. Der Schlupf der Eirauen erfolgt temperaturabhängig nach 12–21 Tagen. Die Raupen sind endophag und kannibalistisch, sogar Präpuppen im fertiggesponnenen Kokon werden als Folge stark ausgeprägter Territorialität aufgefressen. Sie können ungewöhnliches Ruheperioden aufweisen und bauen „falsche Kokons“, möglicherweise um Räuber oder Parasitoiden zu verwirren. Normalerweise haben sie 9 Raupenstadien, gelegentlich auch nur 7 oder 8, wobei ein dramatischer Größenzuwachs stattfindet (von ca. 0,73 cm beim Schlupf bis etwa 9 cm ausgewachsen), der sich auch in bemerkenswerter Zerstörungskraft niederschlägt. Die Gesamtdauer der Larvalzeit ist lang, zwischen ca. 10,5 Monaten bei einjähriger Entwicklung und ca. 18,5 Monaten bei fast zweijähriger Entwicklung. Die Raupen bohren in verschiedenen Teilen der Palmen, meist in Abhängigkeit von der erreichten Körpergröße, wobei sie sich in der Regel in den obersten Teilen der Pflanze aufhalten. Normalerweise verlassen sie ihre Wirtspflanze nicht, bevor sie ausgewachsen sind. Das Präpuppenstadium ist lang und besteht aus 2 Phasen: Erstens eine zeitlich sehr variable Phase vor dem Kokonbau, zweitens dann die Phase, in der die Präpuppe sich im Kokon zur Puppe umwandelt; dies dauert zwischen 17 Tagen im Frühling und 9 Tagen im Sommer. Die Kokons (Durchschnittslänge 5,8 cm) sind sehr fest und innen glatt mit Seide und Sekreten bedeckt; außen werden Teile der Palmen angesponnen, die den Kokon wirkungsvoll tarnen. Puppen, die bereits Mitte März auftraten, hatten eine Puppenruhe von durchschnittlich 66 Tagen, Puppen aus der ersten Aprilhälfte von 52 Tagen, solche aus der ersten Julihälfte nur von 43 Tagen. Die Imagines sind tagaktiv. Die ♂♂ (die etwas weniger häufig als ♀♀ auftreten, im Verhältnis 1:1,19) sind sehr territorial und fliegen bei

heißem sonnigem Wetter. Der Flug ist kraftvoll, schnell und reißend (als Schätzung: 20 m/s), und sie können für einige Sekunden in der Luft schwirrend stehenbleiben. Die Flugbahn ist meist geradlinig, obwohl auch häufig Rechts-links-Schwenkungen vorkommen und dabei der Körper sichtbar ausbalancierend eingesetzt wird. Die Falter fliegen immer wieder kleine Runden, immer von denselben Ruheplätzen aus. Ihre Orientierungsfähigkeiten sind bemerkenswert; sie können über Hunderte von Metern wegfiegen, minutenlang und weit aus der Sicht des Beobachters, kommen aber wieder zum identischen Sitzplatz zurück. In Gefangenschaft lebten die ♀♀ durchschnittlich 14,1 d, die ♂♂ 23,8 d, und beide Geschlechter konnten nicht bei der Nahrungsaufnahme beobachtet werden. Vorläufige Beobachtungen zeigten, daß die Geschlechtererkennung anfangs rein optisch ist. Die ♀♀ fliegen durch geeignete Habitate, bis sie von einem patrouillierenden ♂ gesichtet werden, ähnlich wie bei vielen Tagfaltern. Die Feststellung, daß Elektroantennogramme von ♂-Antennen, die mit Hexanextrakten von ♀-Ovipositoren angeblasen wurden, eine positive und starke Antwort zeigten, läßt vermuten, daß bei *P. archon* zumindest ein auf kurze Strecken wirksames Nahbereichspheromon zur Geschlechterfindung besitzen, während die sonst übliche Langstreckenwirkung des ♀-Pheromons offenbar durch optische Geschlechterfindungsmechanismen ersetzt wurde. Das Paarungsverhalten im Freiland wird erstmals beschrieben. Die ♀♀ legen die Eier einzeln mit dem langen, teleskopartig ausfahrbaren Ovipositor unauffällig und sehr schnell. Die meisten Eier finden sich in den netzartigen Fasergeflechten der Palmkronen; sie sind nicht angeklebt, sondern liegen lose relativ tief in diesen Fasergeflechten. ♀♀, die bekanntermaßen keine Eier gelegt hatten, zeigten beim Sezieren etwa 140 Eier im Hinterleib. Imagines können ab Mai bis Ende September festgestellt werden mit dem Schwerpunkt im Juni/Juli; in Mai, August und September können nur wenige gesehen werden. Sich entwickelnde Eier treten von Ende Mai bis Mitte Oktober auf. Das Raupenstadium ist das längste und komplexeste der Stadien. Es ist das einzige überwinterungsfähige Stadium; im Winter treten fast alle Größenstadien in Palmen auf einschließlich erwachsener L₉-Raupen im Präpuppenstadium. Die meisten Raupen entwickeln sich einjährig, obwohl es auch eine zweijährige Entwicklung gibt. Lebende Puppen im Kokon findet man zwischen Mitte März und Mitte September. Der Lebenszyklus von *P. archon* in Katalonien dauert bei einjähriger Entwicklung durchschnittlich 389 Tage (= 12,8 Monate), bei zweijähriger Entwicklung 673 Tage (= 22,1 Monate). *P. archon* ist nach bisheriger Kenntnis offenbar ausschließlich auf Palmen (Arecaceae) spezialisiert, akzeptiert aber aus dieser Familie eine breite Vielfalt von Gattungen. Über natürliche Feinde ist bisher weder in der Neotropis noch in Europa viel bekannt; einige Funde von leergefressenen Eiern in Katalonien lassen jedoch Hymenopteren-Eiparasiten oder eianstechende Hemipteren vermuten. Längere Frostperioden über mehrere Tage lassen die Mortalität der überwinternden Raupen in den Palmen ansteigen; jedoch ist diese Art an das mediterrane Klima insgesamt gut angepaßt. Ein befallener Palmstamm läßt sich erkennen durch: 1) Austritt von Sägespänen in der Palmkrone oder am Stamm; 2) Vorhandensein von durchlöcherten oder angefressenen Palmblättern (wenig spezifisch); 3) Vorhandensein von Ganglöchern (axial oder transversal) im Palmstamm, sichtbar sobald dieser in Scheiben gesägt wird; 4) abnormale Entwicklung von Seitenknospen; 5) Deformierungen und unnormaler Drehwuchs von Palmstämmen; 6) Absterben und Austrocknen von Palmen, insbesondere beginnend mit den obersten Blättern. Als mögliche Bekämpfungsmaßnahmen (neben dem Roden und Verbrennen der Stämme) wurden bisher einige chemische Mittel

ausprobiert; beste Erfolge erzielte man mit systemischen oder Kontaktinsektiziden (Organophosphate wie Chlorpyrifos [48 %, Dosis 200 ml/HL], Acephate [75 %, Dosis 150 g/HL] und Dimethoat), die in die Krone und auf den Stamm gespritzt wurden.

El cástnido barrenador de las palmeras, *Paysandisia archon* (BURMEISTER, 1880), en Europa: Biología comparada, condición de plaga y posibles métodos de control (Lepidoptera: Castniidae)

Resumen: *Paysandisia archon* (BURMEISTER, 1880) es un lepidóptero Castniidae Neotropical que ha sido recientemente introducido en Europa (desde Argentina), donde se ha convertido en una preocupante plaga de las palmeras. Desde que se informó por primera vez de su presencia en Cataluña (España) en marzo de 2001, también se ha hallado en la Comunidad Valenciana y Balear (España), en varios Departamentos del sudeste de Francia, en Italia (Sicilia, Campania, Lazio, Marche) e incluso en Sussex (Reino Unido). Sus estadios y ciclo biológico no eran conocidos con detalle y se presentan aquí, comparándolos con los de otros cástnidos considerados como plaga — principalmente *Telchin licus* (DRURY, 1773), *Castniomera atymnius* (DALMAN, 1824) y *Eupalamides cyparissias* (FABRICIUS, 1776). El huevo de *P. archon* (la mayoría entre 4,4 y 5,2 mm de longitud) es fusiforme, pareciéndose a un grano de arroz, presenta de seis a ocho estrías longitudinales con aerópilos asociados, el micrópilo se halla en el extremo del eje largo; la incubación dura entre 12 y 21 días, en función de la temperatura. Las larvas son endófagas; caníbales (afectando incluso a las larvas prepupales en el interior de sus capullos completamente formados), principalmente como resultado de su territorialidad; experimentan periodos de letargo poco usuales y fabrican “capullos falsos”, con toda probabilidad para confundir a predadores/parasitoides. Generalmente pasan por nueve estadios (ocasionalmente siete u ocho), aumentando su tamaño de forma extraordinaria (desde aproximadamente 0,73 cm al nacer, hasta 9 cm en el último estadio), creciendo en la misma proporción su poder destructor. El estadio larvario completo es bastante largo (aproximadamente 10,5 meses en larvas que experimentan un ciclo anual y 18,5 meses en aquellas que lo experimentan casi bianual). Las larvas pueden hallarse realizando túneles en diferentes partes de las palmeras, lo cual depende en buena parte del tamaño larvario, aunque siempre se encuentran en la corona o cerca de la misma; normalmente no abandonarán la palmera hasta alcanzar el estadio adulto. El estadio larvario prepupal es largo y complejo, constituido por dos periodos. El primero es previo a la realización del capullo y su duración es muy variable. El segundo es posterior a la realización del capullo y contabiliza el tiempo pasado por la larva en el interior de aquél antes de convertirse en pupa; este tiempo es de unos 17 días a principios de primavera, pudiéndose acortar hasta tan sólo 9 días a principios del verano. Los capullos (con una longitud media de 5,8 cm) son robustos, con paredes interiores finalmente recubiertas por una capa de seda y mucus, y con paredes exteriores cubiertas de forma basta con fragmentos de fibras de palmera; lo que los hace muy crípticos. Las pupas formadas en la segunda mitad de marzo tardaron una media de 66 días para completar su metamorfosis hasta convertirse en adultos; aquellas formadas en la primera mitad de abril tardaron 52; mientras que las formadas en la primera mitad de julio tardaron 43. Las mariposas son de vuelo diurno. Los machos (que son ligeramente menos abundantes que las hembras, en la relación de 1:1.19) son muy territoriales y vuelan en tiempo cálido y soleado. Su vuelo es muy potente, rápido y súbito (se estiman unos 20 m/s), siendo

capaces de mantenerse suspendidos en el aire por unos pocos segundos; la trayectoria del vuelo es generalmente rectilínea aunque la mariposa balancea su cuerpo para realizar giros a derecha/izquierda. Vuelan una y otra vez sobre áreas más bien pequeñas. Su capacidad de orientación es extraordinaria, siendo capaces de volar centenares de metros, desaparecer de la vista del observador por varios minutos y regresar exactamente a la misma hoja de la misma palmera de la que habían partido. En el laboratorio, las hembras vivieron una media de 14,1 días mientras que los machos vivieron 23,8, y ambos sexos parecen no alimentarse en este estadio. Estudios preliminares indican que el reconocimiento sexual parece ser visual de entrada. Las hembras simplemente se mueven (vuelan) dentro del hábitat apropiado hasta que son vistas por un macho expectante — de forma parecida a como lo hacen las mariposas de día (ropalóceros). El hecho de que electroantenogramas realizados usando extractos hexánicos de oviposidores de hembras determinaran una respuesta positiva y significativa en antenas de machos, parece indicar que *P. archon* tiene por lo menos una feromona de corta distancia emitida por las hembras, mientras que las de larga distancia, es decir aquellas usadas por otros heteróceros para atraer machos conspecíficos a distancias más largas, podrían estar ausentes en *P. archon* y reemplazadas por la atracción visual. La cópula en la naturaleza ha sido observada y descrita por primera vez. Las hembras ponen los huevos de forma individual (a través de su largo y extensible ovipositor) de una forma rápida y poco perceptible, en las mallas de fibra más cercanas a la corona o que forman parte de la misma. Estos, no están adheridos a las fibras y permanecen sueltos dentro de sus espesas capas (1-2 cm en el interior). Algunas hembras diseccionadas, de las que se sabía no habían depositado huevos, presentaron alrededor de 140 huevos. En referencia al ciclo biológico, los adultos aparecen en la naturaleza a mediados de mayo y desaparecen a finales de septiembre, con un pico de población durante los meses de junio y julio; los avistamientos de adultos en mayo, agosto y septiembre son bastante más raros. Los huevos pueden encontrarse desde finales de mayo y hasta mediados de octubre. El estadio larvario es el más largo y complejo de todos los estadios de *P. archon*, siendo el único que inverna. Durante el periodo invernal, en la naturaleza, pueden hallarse larvas de casi todos los estadios en el interior de las palmeras, inclusive larvas prepupales de noveno estadio. La mayoría de las larvas experimentará un ciclo de un año, aunque un segundo grupo experimentará un ciclo de casi dos años. Los capullos pueden hallarse desde mediados de marzo hasta mediados de septiembre. En definitiva, el ciclo biológico de *P. archon* en Cataluña comprende, de huevo hasta huevo, una media de 389 días (12,8 meses) en especímenes de ciclo anual y una media de 673 días (22,1 meses) en especímenes de ciclo bianual. Las larvas de *P. archon*, al parecer, se han especializado en alimentarse de Arecaceae (palmeras) puesto que todas las plantas hospedantes sobre las que han sido citadas pertenecen a esta familia de monocotiledóneas; sin embargo, dentro de ella, las larvas pueden atacar a distintas especies y géneros. En cuanto a los enemigos naturales, tanto en Europa como en el neotrópico, no existen datos concretos todavía; sin embargo, fueron encontrados algunos huevos vacíos en una plantación de palmeras cercana a Girona (Cataluña), que sugieren la existencia de ataques por parte de himenópteros parasitoides de huevos o hemípteros oófagos. Si las temperaturas mínimas del invierno descienden de forma considerable durante varios días, pueden provocar la muerte de una parte importante de las orugas invernantes; de todas formas, debe considerarse esta plaga como adaptada a las condiciones climáticas de la zona mediterránea. Los síntomas de infesta-

ción sobre palmeras por parte de *P. archon* son: (1) presencia de serrín sobre la corona y/o tronco de la palmera; (2) presencia de hojas perforadas o mordisqueadas (no específico); (3) presencia de agujeros de galería (axiales y transversales) en el interior del tronco (observable cuando éste es cortado en rodajas); (4) desarrollo anormal de brotes axilares; (5) deformaciones y torceduras anormales del tronco; (6) secado anormal de las palmeras (especialmente las hojas centrales). En relación a las medidas de control, de momento tan sólo se han probado aquellas que establecen el uso de productos insecticidas (además del arrancado y quemado de palmeras infestadas); se han obtenido buenos resultados mojando la corona y el tronco de la palmera con insecticidas organofosforados de contacto y/o sistémicos (Clorpirifós, Acefato y Dimetoato); los mejores resultados se obtuvieron usando Clorpirifós 48%, a una dosis de 200 ml/Hl o Acefato 75% a una dosis de 150 g/Hl.

Introduction

Paysandisia archon (BURMEISTER, 1880) is an attractive castniid moth (Figs. 1a, b) whose presence in Europe was first indicated as having a well-established population in Catalonia, in northeastern Spain (AGUILAR et al. 2001, SARTO I MONTEYS 2001, 2002). Soon afterwards, its presence was also reported from southern France (SARTO I MONTEYS & AGUILAR 2001, DRESCHER & DUFAY 2001). Its larvae are endophagous and feed inside the trunks and branches of several species of palm trees (Arecaceae). Infested trunks may be severely damaged because of the galleries produced by the larvae as they bore through them, as well as by secondary infections by fungi and other microorganisms that may result. Although this species is not considered to be a palm pest in its native habitat (northeastern Argentina, Paraguayan Chaco, western Uruguay and the southernmost state of Brazil, Rio Grande do Sul, all of which are located between the parallels 25° and 35°, just south of the Tropic of Capricorn), it is certainly a pest in Spain, France and Italy.

The present paper deals with the comparative biology and life history of this moth, including many ecological and behavioural traits of its larvae and adults, its larval foodplants, pest status, introduction and spread in Europe, natural enemies, the damage it inflicts to palm trees and possible methods of control. The morphology and biometry of the egg was studied by SARTO I MONTEYS et al. (2005), whereas aspects concerning the species' discovery, description and taxonomy were thoroughly covered by one of us (SARTO I MONTEYS 2002).

Material and methods

All data presented here result from numerous biological observations obtained through three continuous years, from November 2000, when larvae of this introduced moth were first found in the province of Girona (Catalonia, Spain), to November 2003.

Eggs and larvae were obtained mostly in the wild (palm groves and nurseries) by thorough examination of palms. To extract the larvae from their galleries, a chainsaw was

used for cutting slices of the affected palm trunks. A compensation system was set up by the Catalanian Department of Agriculture to compensate the growers for the damage produced due to this necessary research.

Larvae were reared in insectaries within fruits, palm trunks and leaf rachises of either *Phoenix canariensis*, *Trachycarpus fortunei* or *Chamaerops humilis* palms. Insectaries were water-sprayed (for maintaining a certain humidity level) every second day in spring and summer, and once a week in autumn and winter. When moving larvae from old to fresh leaf rachises, a hole (corresponding ca. to the actual larval diameter and length) was bored into one of the ends of the fresh rachis using a drill; then the larva's rear end was introduced into it, and then the caterpillar naturally moved backwards into the hole until hiding itself completely. Later a ball of cellulose paper was used to plug the hole exit. The larva remained in the hole and soon started tunnelling again, expelling new frass through the former hole exit, pushing out the cellulose ball. This method was more efficient (in terms of diminishing mortality) than simply excavating a small pit into the fresh rachis or just leaving the larva to do everything itself.

Another successful rearing method used was that of mesh wrapping smaller pieces of *T. fortunei* cores (length 18–10 cm, diameter 11–10 cm) containing one or few larvae. Those meshed bags were kept in insectaries placed in the lab and also outdoors (Fig. 2)

Observations of the adult behaviour in the wild were made fortnightly from 8. v. through 27. vii. 2003 on an experimental plot close to Girona (Catalonia, Spain). It had an area of 2400 m², rectangular shaped, and contained 342 Chusan palm trees, *T. fortunei*, arranged in rows, 0.5 to 2.5 m high, mostly around 1.5 m; 92 % of the palms hosted larvae of *P. archon*, and 20 % of the palms were already dead due to heavy castniid attack. The plot was isolated and bounded by a road and horticultural and alfalfa plantations. It was not in good cultivated condition, as the undergrowth was overgrown by weeds, sometimes higher than the shortest palm trees; the occasional pulling up of dead palms had generated some clearings within the plot.

The names of all the species of Castniinae cited are given according to the checklists of LAMAS (1995) for Castniini (Neotropical castniids) and NIELSEN et al. (1996) for Synemonini (Australian castniids).

Life history

HOULBERT (1918), thanks to the information given to him by Monsieur Joseph PETIT, a Frenchman who lived in Paysandú (Uruguay) and who had presented OBERTHÜR with the material that allowed the latter to describe *Castnia josepha* in 1914 (a synonym of *archon* BURMEISTER, 1880) (see SARTO I MONTEYS 2002 for full details), provided for the first time some data on the biology and host-plant of *P. archon*. Because of its high historical value we

reproduce HOULBERT's text here: "Le *P. josepha* vole très rapidement, à la façon des Sphinx, mais en plein midi, autour des Palmiers à feuilles épineuses [*P. canariensis*] à l'intérieur desquels vit la chenille qui est blanchâtre et à tête brune. L'éducation de la chenille est difficile à réaliser, mais la recherche des cocons, presque toujours fixés à l'aisselle des pétioles, fournit aux chasseurs le moyen d'obtenir rapidement un grand nombre de papillons vivants. Les oeufs sont pondus sous les feuilles; à l'éclosion, les petites chenilles gagnent l'intérieur des troncs où elles creusent, dans la moelle, de larges galeries, qui s'entrecroisent dans tous le sens et qui ne sont pas sans causer quelque préjudice aux palmiers."

Later, BOURQUIN (1930, 1933, 1944) briefly described the *archon* egg, larva and pupa, figuring the final larva and all other life stages, and provided some biological data, mentioning that it had the potential to become a serious pest of palms (see below).

The egg stage

The egg of *P. archon* (Fig. 3) is a typical castniid egg, fusiform, resembling a rice grain, bearing six to eight raised longitudinal ridges which have associated aeropyles along their length, with the micropyle at one end of the long axis. Their colour, when freshly laid, is creamy pink or light brown, agreeing with the observations of BOURQUIN (1930) and DRESCHER & DUFAY (2001), becoming rosy brown as the days pass. The egg shell of hatched eggs appears dull white when seen on the fibre meshes of the palm; however, when illuminated under the stereomicroscope it shows a greenish tinge. Its length is 4.69 ± 0.37 mm ($n = 163$), samples ranging from 5.45 to 3.67, the majority measuring between 4.4 and 5.2 mm. Its width, on the widest section, is 1.56 ± 0.11 mm ($n = 118$), samples ranging from 1.94 to 1.21, the majority measuring between 1.50 and 1.60 mm. Full details on the morphology and biometry of the egg were thoroughly covered elsewhere (SARTO I MONTEYS et al. 2005).

The chapter "Oviposition behaviour and fecundity" below deals with how and where on the palms, eggs are laid by *P. archon* ♀♀.

As for the duration of embryonic development, i.e. from egg laying to egg hatching, from a sample of 119 eggs, with known oviposition dates and maintained in the lab (temperature 26–30°C), it was established that 96.6 % of those hatched after 12 to 14 days whereas 3.4 % hatched in 15 days. However, three eggs collected in the wild on 4. vi. 2002, and kept in the lab at slightly lower temperature (22–24°C) hatched in 20 days; although the exact oviposition date in the wild was not known, it is likely that this was very close to the date they were found. DRESCHER & JAUBERT (2003) reported this as being from 14 to 21 days (sample size and mean not specified; lab temperature $24 \pm 2^\circ\text{C}$). As with most lepidopterans, temperature plays an important role in the duration of the embryonic development. Data retrieved from the internet (PATTON & PERRY 2002) indicating that hatching

in *P. archon* occurs only 2–3 days after laying, are groundless (see SARTO I MONTEYS 2003).

Previous original data on hatching times for other Neotropical castniids are scarce and summarized in Table 1. Other authors (ESQUIVEL 1981 for *T. licus* (DRURY, 1773), HUGUENOT & VERA 1981 for *E. cyparissias* (FABRICIUS, 1776) and MILLER 1986 for *T. licus* and *E. cyparissias*) simply used data from authors mentioned in Table 1.

Table 1: Original data on hatching times for Neotropical castniids other than *P. archon*. — * = Note: ESQUIVEL (1981) stated that research carried out in Panamá demonstrated that *T. licus* and *C. atymnius* were in fact the same species. However, both are kept as separate species by MILLER (1995) and LAMAS (1995), although the latter suspects they are indeed conspecific.

Castniidae species	Egg incubation period stated	Source
<i>Telchin licus</i> (DRURY, 1773)*	11 d or more	QUELCH (1910)
	7–14 d	SKINNER (1930)
	10 d	RISCO (1978)
<i>Castniomera atymnius</i> (DALMAN, 1824)*	18–26 d	GALLEGO (1940)
	10–14 d with a mean of 11.85 d	LARA (1964)
<i>Eupalamides cyparissias</i> (FABRICIUS, 1776)	14–22 d with a mean of 16.7 d	KORYTKOWSKI & RUIZ (1980)

MILLER (1986) pointed out that during the course of attempting to rear some species (*T. licus*, *E. cyparissias* and *Prometheus cochrus* (FABRICIUS, 1787)), it was determined that additional moisture was necessary in the rearing containers to prevent further desiccation of the egg chorion and to aid in keeping it pliable so that the first instar larva could hatch. We did not experience such a need with the eggs of *P. archon* reared by us; they were kept in rearing cages at ambient moisture (around 60 % RH); no additional moisture was added and all eggs hatched successfully.

The larval stage

Larval emergence

P. archon larvae emerge from the egg by gently splitting the chorion along the membrane contacting one of the longitudinal ridges, always on the half closer to the micropyle, one end of the split being just below the micropyle, the other end found about one-fourth to one-third the egg length. This operation, i.e. since the larval mandibles start splitting the chorion until the larva fully frees itself from the egg, may last for two to fifteen minutes, most larvae accomplishing it in about five minutes (Figs. 4a–4d). Immediately after emergence the larvae start looking for food and shelter, both being obtained by boring into the hostplant; unlike other lepidopteran larvae, they do not eat the chorion. This behaviour had already been described by LARA (1964) in *C. atymnius* (DALMAN, 1824), by ESQUIVEL (1981) in *T. licus* and by MILLER (1986) in

T. licus, *E. cyparissias* and *P. cochrus*, so most likely it is widespread among castniids.

Larval endophagous/exophagous condition

Once into the hostplant the larvae will commence tunnelling and, normally, will not abandon it until the adult stage is reached. Thus, the larvae of *P. archon* are endophagous most of their lives, being exophagous only during the very short time needed from eclosion to entering the hostplant. DRESCHER & JAUBERT (2003) reported that a set of newly emerged larvae took from 5 seconds to 3 minutes to enter the palm.

However, in other castniids, the time elapsing between eclosion and hostplant penetration can be longer, although penetration usually takes place in the first larval instar. For example, in the Oil Palm Borer, *E. cyparissias*, KORYTKOWSKI & RUIZ (1980) pointed out that usually the first instar larva consumes a small basal portion of several fruits of the cluster before penetrating into its rachis. In the Giant Cane Borer, *T. licus*, SKINNER (1930) said that its first act after emergence is to work its way down, between the leaf-sheath and the cane, to ground level, where a small cavity is eaten out in the rind of the cane and in this, the first few days of larval life are spent, after which it then commences tunnelling into the heart of the cane. In the Banana Stalk Borer, *C. atymnius*, LARA (1964) reported that the first instar larva is fully exophagous, and can be found either scratching outer tissues of healthy, second lowest leaf-sheaths of banana suckers or feeding upon lowest leaf-sheaths of suckers.

These observations lead to the conclusion that first instar larvae of castniids, including *P. archon*, can be partly or fully exophagous. Also, other behavioural and morphological traits found in known first instar larvae of castniids support this initial exophagous condition versus the endophagous one of later instars (MILLER 1986). For instance, newly emerged larvae of *P. archon* are very mobile and lucifugal, moving quickly in search for concealed positions and food, sometimes climbing down, held by silk threads they produce, altogether helping the insect to quickly locate an appropriate spot to initiate boring and feeding. It is in this phase when they are most vulnerable to contact insecticides sprayed on the palm. Apart from their light brown head capsule, their colour is beautifully rosy after emergence (exceptionally only the dorsal vessel is rosy, the rest of the body being whitish), their chaetotaxy is different in the number and especially the length of the setae (much longer), and they do not present cuticular spinules. However, even through the first instar, the rosy colour fades towards whitish and the long straightlined setae become shorter because of multiple folding due to constant friction against the gallery walls where the larva lives. After the first moult, mobility diminishes notably, the colour of the larva becomes ivory white, chaetotaxy changes and the setae become much shorter, cuticular spinules appear; all these new traits are retained throughout the remaining larval stage, clearly

indicating an endophagous condition. Earlier instars show a blackish dorsum as a consequence of the blackish longitudinal dorsal vessel clearly seen from outside the body; later instars turn more intense ivory white and the dorsal vessel is less obvious. Light brown cuticular spinules on the dorsum of the prothoracic segment form an "M" mark, more obvious in mid and later instars.

Larval instars, their length and moulting pauses

The number of instars undergone by larvae of *P. archon* seems to be nine (Fig. 5). This conclusion was reached after thorough examination and statistical analysis of up to seven morphological characters in a sample of 328 larvae obtained directly from infested palms plus five first instar larvae obtained from eggs also collected in the wild. These data will be presented in a separate paper. Notwithstanding that, data obtained from larvae reared in captivity seemed to indicate that pupation is also possible once the larva has reached the 7th instar. As far as we know, detailed data on number of instars undergone by other castniid larvae are only those of LARA (1964) in *C. atymnius* and KORYTKOWSKI & RUIZ (1980) in *E. cyparissias*. The former found that larvae of *C. atymnius* go through eight, nine or ten instars, with nine being the most common (71.4 % of the larvae analyzed) ($n = 14$) and this variation not being correlated to sex. The latter reported that larvae of *E. cyparissias* go through 15 instars; however, by closely looking at the results presented and the difficulties encountered while rearing the larvae, it is obvious that these authors overestimated this number, which most likely will fall closer to that found by LARA and by us. In any case, castniids seem to be one of the lepidopteran families whose larvae undergo more moults. RICHARDS & DAVIES (1977) reported that within the order Lepidoptera, larval instars are generally from two to nine according to species.

P. archon larval feeding begins shortly after eclosion and continues until the larva reaches the prepupal stage (when feeding definitively stops), being interrupted by all moults. When the larvae enter a premoulting period they stop feeding and build a simple and loose chamber with chewed palm fragments and silk; sometimes this chamber is not very conspicuous. In there, the process of moulting will take place. We noticed that moulting pauses last for from about one to three days; the older the larva, the longer it takes. After the exuviae are shed a resting pause follows and the larva resumes feeding by normally (but not always) eating first the old skin. Some larvae may also try to eat their old head capsules, as we have sometimes recovered only fragments of them.

It has also been observed that, sometimes, larvae taken from their galleries in the wild and placed in captivity in insectaries (thus undergoing stress), quickly enter a moulting period, which appears to be hasty or premature. These moults might well turn out to be supernumerary moults, as already known in other lepidopteran larvae. Indeed, under adverse conditions (nutritional or

other), the number of larval instars in some Coleoptera and Lepidoptera can be increased (sometimes greatly), although there is little growth in size (RICHARDS & DAVIES 1977).

Going through these nine instars, the larvae of *P. archon* increase in size dramatically, and so does their destructive power. After emergence, the body length is 7.3 ± 2.2 mm ($n = 5$), the width of the head capsule at the widest part being 1.00 ± 0.10 mm ($n = 5$). When full grown, but before entering the prepupal stage when some contraction takes place, the larva may reach a body length of 9 cm, width of 1.5 cm at mid-length, and the width of the head capsule at the widest part being 7.84 ± 0.34 mm ($n = 52$).

As for the length of each larval instar, our data are not conclusive due to the small sample size. Because the total larval period of *P. archon* is quite long (10.5–18.5 months, see life cycle below for details) and because of their larvae being cannibalistic and going through lethargic periods, rearing larvae on fresh palm chunks from eclosion to pupation is very complicated, resulting in high

larval mortality, especially in earlier instars. An artificial diet might help to overcome this, but it was not tried at this stage. We closely followed in captivity the development of three larvae, one hatched on 9. VIII. 2002, two on 11. VIII. 2002; of the latter one escaped in x. 2002. The two remaining larvae hatched to the adult on 4. VIII. 2003 and 14. VIII. 2003, and their larval stage lasted 321 days and 319 days respectively. Therefore, these two larvae had a one-year cycle, underwent only seven instars (instead of nine), behaved as those in group A (as described in the section “Unusual lethargic periods” below), and their specific instar lengths were those shown on Table 2.

Data on larval stage duration for Neotropical castniids other than *P. archon* are summarized in Table 3. They refer to the full larval stage, i.e. including the prepupal period of the larva.

A striking feature concerning the length of the larval stage is the wide gap between the minimum and the maximum lengths reported intraspecifically, especially keeping in mind that, according to ESQUIVEL (1981), *T.*

Table 2: Length of larval instars in days undergone by *P. archon* (referred only to one-year cycle larvae, seven-instar larvae, group A larvae; see text for details).

Larval instar	Length [days]	Larvae observed	Dates	Observations
L ₁	11–12	3	9. VIII. to 20. VIII. 2002	
L ₂	12–13	3	21. VIII. to 2. IX. 2002	
L ₃	16–17	3	3. IX. to 18. IX. 2002	
L ₄	25	2	19. IX. to 13. X. 2002	
L ₅	40	2	14. X. to 24. XI. 2002	
L ₆	123	2	25. XI. 2002 to 29. III. 2003	Larvae did not grow and stayed lethargic from 5. XII. 2002 to 12. III. 2003, when they resumed activity
L ₇	92	2	30. II. to 30. VI. 2003	Larvae entered a lethargic period around late April, which was not abandoned until initiating construction of the cocoon on 23. VI. 2003
L ₈	—	—	—	
L ₉	—	—	—	
Total	319–321			

Table 3: Data on larval stage duration for Neotropical castniids other than *P. archon*.

Castniidae species	Larval stage duration (including prepupal period)	Source
<i>Telchin licus</i> (DRURY, 1773) (“Giant Cane Borer”)	“at least 8 weeks” under favourable conditions	SKINNER (1930)
	6–10 months	RIBEMBOIN (1964)
	2–3 months	BATES (1965)
	110 d	RISCO (1978)
	6–10 months	MENDONÇA (1982)
<i>Castniomera atymnius</i> (DALMAN, 1824) (“Banana Stalk Borer”)	“it does not exceed 9 months”	GALLEGO (1940)
	60.9 to 93.2 d, mean 73.62 d (i.e. 2–3 months; $n = 233$ observations)	LARA (1964)
<i>Eupalamides cyparissias</i> (FABRICIUS, 1776) (“Oil-Palm Borer”)	161 to 423 d, mean 249 d (i.e. 5–14 months)	KORYTKOWSKI & RUIZ (1980)

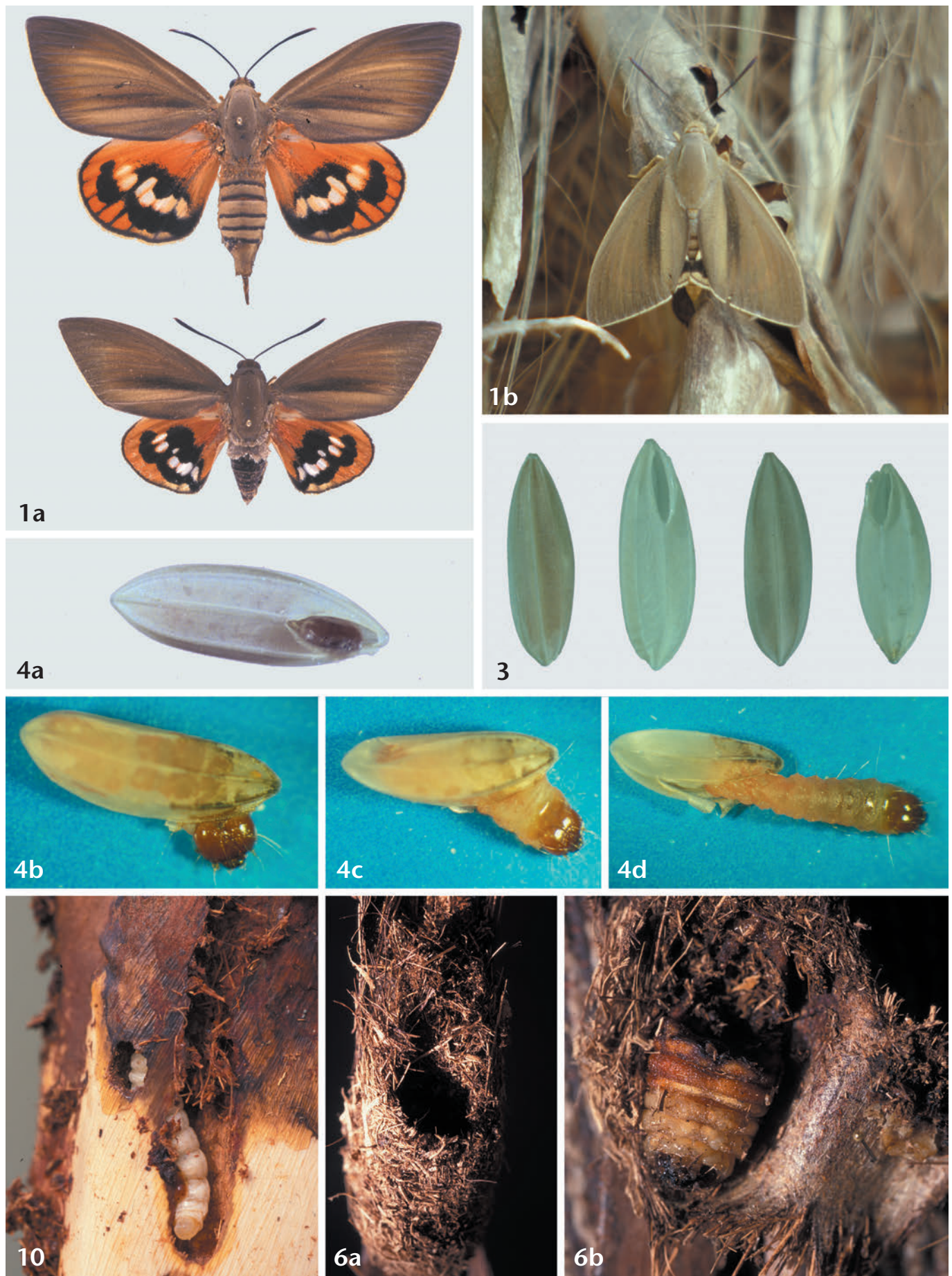


Plate 1: *Paysandisia archon* (BURMEISTER, 1880). **Fig. 1:** Imagines of *Paysandisia archon*. **Fig. 1a:** ♀ (top) and ♂ (bottom). **Fig. 1b:** ♀ cryptically resting on a palm crown. **Fig. 3:** *P. archon* eggs (two hatched — see opening close to the micropylar pole — and two unhatched). **Fig. 4:** Series showing the eclosion of a *P. archon* larva from the egg. **Fig. 6:** Cannibalized cocoons. **Fig. 6.a:** Empty cocoon. **Fig. 6.b:** Cannibalized prepupa inside cocoon. **Fig. 10:** Medium sized larva boring through the core of a *T. fortunei* palm trunk. The core is already decaying.



Fig. 2: Rearing of *Paysandisia archon*. **Fig. 2a:** Meshed bags containing one or a few pieces of *T. fortunei* palm trunk chunks used for rearing one or a few larvae of *P. archon*. They were used outdoors (hanging, photographed) and also indoors (in insectaries). **Fig. 2b:** Cocoons contained in meshed bags.



Fig. 5: Nine larval instars of *P. archon*. **Fig. 7:** Black necrotic spots on the integument of a *P. archon* larva.

licus and *C. atymnius* are the same species. The reason for this is not known. ESQUIVEL (1978) found in *T. licus* that larvae badly fed or lacking food could get into a phase of “suspended animation” that allows them to survive without feeding for many months, to continue their development when food is found; therefore the nutritional conditions of the larva would determine the duration of this stage.

In *P. archon*, the larval stage duration, including the prepupal period, is ca. 10.5 months in larvae having a one-year cycle and ca. 18.5 months in larvae having an almost two-year cycle. Therefore, our data do not support the estimate made by DRESCHER & JAUBERT (2003), who gave no evidence that this stage might take up to two or three years in the wild, depending on climatic conditions.

Larval overwintering and resistance to cold

Overwintering in *P. archon* is exclusively undergone by the larval stage; all the other stages are absent through the winter time. During this period nearly all larval instars can be found within the palms in the wild, including prepupal ninth instar larvae. The latter, though, will not begin making the cocoon until the winter is over, or almost over (see life cycle below for details).

It has been observed in the lab that *P. archon* larvae are able to cope with continuous moderate cold for long periods as long as they remain within their galleries in the palm trunk. For instance, a 22 cm (diameter) × 30 cm cylinder of cut palm trunk of the Mediterranean Fan Palm, *C. humilis*, collected in an infested nursery near Girona on 28. II. 2002, was immediately refrigerated (6–7 °C) and kept so until 7. VII. 2002, i.e. during 130 continuous days. When the piece was taken from the refrigerator and thoroughly inspected, a third instar larva was found, nearly motionless but in good condition. This is an indication that *P. archon* larvae overwintering in the wild should have no real difficulty in overcoming such a cold season in the Mediterranean area, where winters are generally mild.

However, very cold temperatures (say, below –5 °C), lasting for several consecutive days, are also recorded in the northern shores of the Mediterranean. Those might increase mortality in the overwintering *archon* larval population sheltered in palm trees. This issue has not been addressed in detail in the present study and

is expected to depend on both the outside temperature in the palm grove and the temperature inside the palm trunk where the larvae overwinter. Also, the latter is expected to vary among different palm species and with the age of the palm tree, i.e. the older the palm, the thicker its palm trunk, and therefore more insulation provided within.

From 1. XII. 2001 to 20. I. 2002 and from 1. XII. 2002 to 20. I. 2003 (i.e. over a period of 51 days), a search for overwintering larvae of *P. archon* was carried out on an infested *T. fortunei* palm plot located in Anglès (Girona). In both searches, 80 and 40 palm trees, respectively, showing evidence of being attacked by *P. archon* larvae, were inspected and all larvae found, dead or alive, were counted. The plot had not been treated with insecticides so one of the possible causes for finding dead larvae at that time of the year was indeed perhaps cold temperatures. Table 4 summarizes the results. Meteorological data were obtained from the weather station at Vilobí d'Onyar, located 12 km west of the experimental plot.

According to the meteorological data shown on Table 4, the 2001–2002 winter was notably more severe than that of 2002–2003. It is also a fact that through the first winter search more larvae were found dead (55%) than through the second one (only 8%), over a similar sample size of about 100 larvae found. Therefore, there is a strong suspicion that severe winters in Mediterranean areas might increase mortality in overwintering larval populations of *P. archon* sheltering within palm trees. However, further detailed research is needed for determining more precise boundaries of the temperature factor, and establishing the role of other possible causes of larval mortality through the overwintering period.

Larval ethology

a) Cannibalism and larval competition

DRESCHER & JAUBERT (2003) reported that in the lab and when too many *P. archon* larvae shared a limited space, they developed a cannibalistic behaviour. We have observed the following while rearing many *P. archon* larvae:

- (i) *P. archon* larvae are cannibalistic in all their instars. Cannibalism does also affect prepupal larvae within their fully formed cocoons (in such a case, the cocoon will be perforated by another larva which will feed on the prepupal larva inside) (see below) (Figs. 6a, b).

Table 4: Overwintering larvae of *P. archon* found dead within *T. fortunei* palm trees standing on a non-treated plot located near Girona (Catalonia, Spain), together with relevant meteorological data.

	Winter search 2001–2002 (carried out on 80 palms between 1. XII. 2001 and 20. I. 2002)	Winter search 2002–2003 (carried out on 40 palms between 1. XII. 2002 and 20. I. 2003)
Days with $T_{\min} < 0^{\circ} \text{C}$	39	25
Days with $T_{\min} < -5^{\circ} \text{C}$	15	5
Consecutive days with $T_{\min} < -5^{\circ} \text{C}$	10 (20.–29. XII. 2001)	5 (11.–15. I. 2003)
Absolute T_{\min} reached (date)	–11.5 °C (25. XII. 2001)	–6.9 °C (13. I. 2003)
Total larvae found (in inspected palms)	107	92
Larvae found dead (%)	59 (55 %)	7 (8 %)

(ii) Contrary to what was reported by DRESCHER & JAUBERT (2003), we concluded that cannibalistic behaviour does not develop as a consequence of too many larvae sharing a limited space but as a result of territoriality (i.e. keeping their galleries free from other fellow larvae) accompanied by the reward of getting some extra protein. No two larvae will occupy the same gallery, as one (generally the bigger) will end up cannibalizing the other. Indeed, we reared many larvae of different instars within the same chunk of palm trunk, where they were very close to each other and, as long as each particular larva remained within its own gallery, cannibalism was very rare. Larvae seem to be very aware of which is their own gallery and the risks of entering alien ones.

However, when the quantity/quality of food is deficient (e.g. when the succulent palm tissue dries up or is invaded by fungus), the larvae may enter other galleries with the goal of cannibalizing its dweller. Indeed, we noticed several times that big pieces of fresh palm trunks (about 22 cm × 40 cm × 22 cm) where we had only placed two or three larvae (so reduced space was not the case) only rendered one larva after a period of about three to four months. The missing larvae had obviously been cannibalized, as they could not escape the insectarium, so that only one survived.

MILLER (1986) first reported cannibalism in castniids for three species she had reared (*T. licus*, *P. cochrus* and *E. cyparissias*), adding that larvae reared together might survive cannibalistic attacks with resultant tumorous growths, although failed to complete development. However, LARA (1964, 1965) referring to *C. atymnius*, and ESQUIVEL (1981) to *T. licus*, did not find cannibalism; they simply mentioned larval competition, indicating that, when together, older larvae always killed, although did not feed upon, younger ones. Regarding *E. cyparissias*, KORYTKOWSKI & RUIZ (1980) did not mention cannibalistic traits.

It is not uncommon to notice black necrotic spots on the integument of some larvae (Fig. 7). We do not know what they are (maybe an epidermal infection by bacteria) or what causes them. Some larvae survive with them and eventually the spots disappear after a moult; however other larvae eventually die. We noticed those black spots seemed to be more common in larvae that had undergone stress periods, as if their immune systems had weakened enough to let them appear. On the other hand, the possibility of being a secondary infection resulting from the wounds produced by a cannibalistic attack can not be ruled out.

In *P. archon*, cannibalism rarely affects cocoons (meaning the prepupal larvae inside) but it occasionally does. When this happens, the cocoon normally shows a big hole on its lower half and the prepupal larva inside lays dead, missing most of its abdomen. On one occasion, in the lab, a mature larva abandoned a host palm trunk

during the course of the night and began eating a hole into one recently formed cocoon (out of several cocoons left loose in the insectary); by the time it was seen it had not yet fully pierced the cocoon wall, so that the prepupating larva inside was not eaten, as we stopped this action. Obviously, mature larvae are capable of detecting prepupal larvae inside their cocoons and occasionally cannibalize them; we have never found cannibalized pupae.

b) Defensive behaviour

The larvae, excluding the first instar, are capable of discharging through the mouth (also a little through the anus) a reddish-brown exudate when they feel threatened or disturbed; this trait had already been reported by SALT (1929) in *C. atymnius* and by MILLER (1986) in *T. licus* and *E. cyparissias*. It has also been noticed that, when threatened (e.g. holding the larva with forceps or fingers), this exudate can be spat out very forcefully by *P. archon* larvae (up to 40–50 cm away in grown larvae!); this “spitting” had also been observed in *C. atymnius* larvae by SALT (1929). In addition to this, they boldly try to bite the object causing the disturbance.

The larvae are lucifugal and actively avoid being in direct light. When taken out of their galleries and placed temporarily in small plastic containers, with cellulose paper layers placed at the bottom, they quickly hide underneath those. When returned to fresh palm trunks, they immediately disappear under the layers of the fibre web that covers them, where will begin tunnelling again. MILLER (1986) reported those traits too with other castniid species.

P. archon larvae move easily forwards and backwards within their galleries when disturbed, and can also turned around, helped with the short spinules mentioned above. Later instars are so stout that it is difficult, with only fingers, to extract them from their galleries when discovered, as they press their bodies onto the tunnel walls and use the numerous dorsal and ventral spinules as micro anchors.

c) “False cocoon” making

The larvae retain frass in portions of the excavated tunnel during development as well as expel it to the outside through the exit. Frass can also be found between layers of the fibre webs that wrap the trunk or blocking one end of the terminal gallery, i.e. that within which the larva will build the cocoon (see below).

Interestingly, sometimes, later instar larvae (not only the last instar), pack the frass in such a way that the resulting mass resembles very much (concerning its whole size, volume and shape) an actual cocoon. When those “false cocoons” appear between layers of the fibre webs that wrap the trunk, apparently with no connection to any gallery, this might represent, in its natural habitat in the Neotropics, a way of confusing likely predators or parasitoids (see natural enemies below). They can also be found blocking one end of the terminal gallery, providing



Plate 2: *Paysandisia archon*. **Fig. 8:** False and true cocoons. **Fig. 8a:** “False cocoon” (made of compacted frass) on a rachis, blocking one end of the terminal gallery (on the left in the photo). The excavated cavity on the right lodged the actual cocoon (removed). **Fig. 8b:** True cocoon, in an outer trunk cavity, found after removing several fibre meshes covering it; see on the right the outing left by the larva (for the exiting pupa) before making its cocoon. **Fig. 9:** First instar larva within a *C. humilis* fruit. **Fig. 9a:** The penetration hole and some frass are clearly visible on the fruit; the larva can be seen by transparency boring within the fruit. **Fig. 9b:** Idem, partly opened fruit, showing the larva inside. **Fig. 11:** Later instar larva of *P. archon*. **Fig. 11a:** Caterpillar removed from its gallery. **Fig. 11b:** Retreating backwards into its gallery. **Fig. 13:** Pupa within cut open cocoon. **Fig. 14:** Dorsal view of pupal abdominal segments showing transversal rows of short spines pointing backwards. **Fig. 15:** Fresh pupal exuvia protruding from a *C. humilis* palm trunk. **Fig. 16:** ♀ long telescopic ovipositor (1.5–2 cm when fully exerted).

some protection to the true cocoon (Figs. 8a, b). Indeed, those false cocoons confused us many times when looking for true cocoons in the trunks.

d) Unusual lethargic periods

By closely following the development of the larvae being reared, we noticed the existence of lethargic periods, which seemed different to the usual ones caused, for instance, by cold temperatures in winter or by normal prepupal periods. To better understand what follows, see also the Life cycle section and Table 7.

Although most larvae undergo a regular one-year cycle and are already full-grown by the end of winter, in March, building their cocoons from mid March to mid April, there are some larvae (albeit a minority) which do not fit this pattern. Indeed, it was noticed that larvae reaching their later instars (9th, 8th or 7th) from mid-April to mid-May, so theoretically capable of building their cocoon soon and becoming an adult in the course of the approaching summer, enter instead a lethargic, mostly non-feeding state, in which they do not grow, shrink a little and turn a bit yellowish, staying virtually motionless within a very secluded location in the gallery they have built. Then, in June, those larvae behave in two different ways.

One group (**group A**) builds their cocoons, and does so normally from mid June to early July (exceptionally up to mid/late July), resulting in adults, through a very quick metamorphosis, during August and September. We noticed most of the larvae doing so were only in their 7th or 8th instar. This behaviour will determine a one-year cycle for the species, with those larvae having overwintered only once, as they hatched the previous year.

A second group (**group B**) stays in the lethargic state they were in before June, and remain so until the end of the coming winter (i.e. until mid March/early April of the next year) when they build their cocoons, yielding adults in May/June; it is not known if they feed a little to gain some weight before entering the prepupal stage at the end of winter. This behaviour will determine an almost two-year cycle for the species, with those larvae having overwintered twice.

Furthermore, larvae that were not yet in their later instars (9th, 8th or 7th) from mid April to mid May (**group C**), did not enter a spring lethargy (like that of groups A and B), and eventually reached those instars in mid June or later in the summer. However, those larvae always delayed their cocoon building until mid March/early April of the next year, entering in the meantime and once full grown (i.e. in their 9th instar), a lethargic state as described above. This behaviour will also determine an almost two-year cycle for the species, with those larvae having overwintered twice.

The reason why those larvae behave differently is poorly understood. It was also noticed that sometimes larvae found hidden in their galleries from June to late July,

being lethargic and in their 7th or 8th instars, began building their cocoon immediately after the disturbance produced by the removal from their former galleries and relocation in another palm rachis. Should the disturbance not have occurred, perhaps they would have remained lethargic, like larvae in the group B; however, most likely because of the disturbance, they behaved as those in the group A. Also, in some cases, it seemed as if this hasty cocoon-building in 7th or 8th instar larvae might be triggered by poor food quality or food shortage, much in the same way hasty moulting occurred in younger instar larvae (see above). Also, the “suspended animation” phenomenon reported by ESQUIVEL (1978) on *T. licus*, i.e. that the nutritional conditions of the larva would determine the duration of this stage (see above for details), does not seem to apply to the *P. archon* larvae reared or found in the wild by us, since they normally had plenty of food, generally in good condition. But, even in those cases when the food quality in the insectaries was bad, larvae did not enter such suspended animation, instead they underwent fasting and lost weight progressively; some also underwent supernumerary moults.

In summary, the above data indicate that, under natural conditions, cocoon-building and subsequent pupation occurs almost exclusively within two periods, the spring one (from mid-March to mid-April) and the summer one (from mid-June to early July, exceptionally up to late July), with a clear concentration in the former. This is in accordance with the scarcity of adults found from late July to late September (see Graphs 2, 3) as they emerge from the few cocoons built from mid June to early July.

Larval location in the palms

P. archon larvae can be found tunnelling in different parts of the palms which largely depends on the larval size. Early instar larvae, because of their much smaller size, can be found, apart from in the trunks, within the fruits of *C. humilis* (Figs. 9a, b) or within the leaf rachises (especially in *P. canariensis* and *Washingtonia filifera*). In *T. fortunei*, for instance, the first instar larvae can bore into the very young, packed and undeveloped palm leaves that spring from the palm crown; recall the eggs had been laid close to this location by the ♀; this piercing becomes later very obvious, as the leaf develops, opens and expands, showing a series of consecutive holes on a circular sector (Fig. 22b).

The bigger the larvae the higher the probability to find them within the trunk. Large larvae will only be found within the trunk. They tend to bore into and remain within the very core of those structures, where the humidity is higher and the temperature more stable (Fig. 10). A cut piece of trunk (diameter 21 cm, length 35 cm) of *T. fortunei* palm kept in a rearing container in the lab can successfully host several larvae for two to three months with virtually no additional care. The multiple layers of fibre webs, tightly packed together around the trunk, keep the humidity inside its core for a long time. Similar results

were obtained using even smaller trunk chunks held by a hanging mesh and placed outdoors; likewise, meshed cocoons, also placed outdoors, successfully rendered the adults (see Figs. 2a, b).

The larva will not normally abandon its palm host until the adult stage is reached. Under very unlikely special circumstances, e.g. food depletion by excess of larvae on the same palm trunk or flooding of palms, the larvae may abandon the palm and wander around looking for another palm. We have occasionally observed in the rearing containers wandering later instar larvae, which when placed on a fresh palm trunk immediately hid themselves underneath the fibre mesh that covers it and disappeared, tunnelling into it. Due to the big size reached by those developing larvae and their ivory white colour, they would be extremely likely to be eaten by predators outside their tunnels (Figs. 11a, b).

In the wild, those galleries within the palm trunks can be quite long. In the Chusan palm, *T. fortunei*, out of 330 infested palms examined (average trunk length being 82.1 cm), the average gallery depth (from the crown) was 22.4 cm, with 80 cm the maximum depth found. Interestingly, most larvae were located at a depth of about 15 cm. The maximum number of larval galleries found in a single palm trunk was 10. In the Mediterranean Fan Palm, *C. humilis*, because of its much shorter trunk, galleries can reach the very bottom of the trunk, i.e. just above the roots, at ground level.

Also interesting is the fact that, in the wild, grown larvae are found oriented head down in their galleries during summer and most of autumn, whereas they reverse direction at the end of autumn and winter and move a few centimeters upwards, probably as a precautionary measure to avoid possible flooding of the gallery bottom by palm exudates or rain water while they are overwintering. In spring, when they prepare for pupation, they move close to the top of the gallery, towards the crown, or stay further down, boring a transversal side gallery that reaches the trunk external surface.

Prepupal larva and cocoon

When fully developed, the larva enters a so-called prepupal stage. This stage normally occurs in the 9th instar (the last), but sometimes it can be in the 7th or 8th (see above). The prepupal stage is spent in three phases:

- (a) Before actually initiating the spinning of the cocoon
- (b) Spinning the cocoon
- (c) Internal sealing of the fully completed cocoon with viscous secretion followed by larval stillness (preparing for the final moult to pupa)

Phase (a) is characterized by the cessation of feeding, body shrinking, slight color changing to pale yellow and tearing off of palm fibres for cavity making. It can last for a few days (in early spring) to nearly 10 weeks (if late spring lethargy occurs) or nearly 22 weeks (if autumn/

winter lethargy occurs) (see unusual lethargic periods above and life cycle below).

Phase (b) is characterized by the actual spinning of the cocoon. To get the cocoon well shaped and structured, fully opaque, the larvae take 7 days.

Phase (c) is characterized by the internal sealing of the cocoon with a viscous secretion followed by larval stillness prior to moulting to pupa. Indeed, once the larva has completely finished building up the cocoon, it secretes a viscous, sticky, substance that spreads over the internal walls of the cocoon; in contact with the air, it soon dries, leaving behind an imperfect, somewhat patchy, internal coating of the cocoon, that might help to further protect it and render it impermeable. After this, the larva stays quiet in the cocoon until its last moult to pupa occurs.

Phase (c) takes around 17 days in early spring although it can be shortened to only 9 days in early summer. This range (17 to 9 days), which largely depends on temperature, falls within the natural situation the larvae will normally encounter in the wild. In artificial conditions, this can be changed. Indeed, two overwintering full grown larvae that made their cocoons in the lab (average 22° C) in mid January (in the cold of the wild these larvae would not have built their cocoons), were transferred (the cocoons) to a non-heated room (16–18° C) and the duration of phase (c) was controlled by cutting a window in the cocoons. It was not until around mid March that these prepupal larvae moulted to pupae, i.e. phase (c) for these two individual larvae lasted somewhere between 56 and 45 days.

In other Neotropical castniids, data are scarce and patchy, as it is not always clear what phase of the prepupal stage (a, b or c, as described above) authors are referring to. SKINNER (1930) reports in *T. licus* that the larva remains in a semi-comatose condition, for a “considerable period” prior to making the cocoon. MILLER (1986), also for *T. licus*, indicates that during the last two weeks prior to making the cocoon, the larvae become quite lethargic and eat little food; in addition she also reports that the prepupal time frame [supposedly that inside the cocoon] is “extraordinarily” long (7–9 days). In *E. cyparissias*, KORYTKOWSKI & RUIZ (1980), say the prepupal period (up to finishing building the cocoon) took 19 days as an average; once inside the cocoon, only from 6 to 8 hours were needed to moult into the pupa. LARA (1964) thoroughly studied this for *C. atymnius*, indicating that the prepupal period from the cessation of feeding until the spinning of the cocoon took from 2 to 4.5 days, after which the prepupal larva remained within the cocoon for from 4 to 6 days until the last larval moult to pupa occurred; thus, the total prepupal period varied from 6 to 10 days. SALT (1929), also for *C. atymnius*, only considered the time spent by the prepupal larva inside the cocoon and reported this was from 4 to 6 days, exactly the same reported by LARA (1964).

As mentioned above, *P. archon* larvae dedicate a considerable amount of time to making the cocoon as well as to

the preceding preparations. First, the larva has to bore a readily accessible tunnel that will allow the pupa to reach the outside after leaving the cocoon. Then it excavates a cavity where the cocoon will be made. Consequently, the cocoon will always be located near/on the surface of the trunk or leaf axillae, very well camouflaged, mainly, when on the trunk, underneath some layers of the fibre webs that surround it. The cavity where the cocoon stays is located at one end of the terminal larval gallery, whereas the other end often appears blocked by a false cocoon or compacted frass also built by the larva (Figs. 8a, b).

In heavily infested palm trees it is possible to find several of these cocoons on the trunk, at close distance to each other, underneath the fibre webs. Once, we found 20 cocoons on a single *T. fortunei* palm tree, although the majority of the palms checked had many fewer than that.

The cocoons are quite stout with inner walls smoothly coated by a layer of silk and mucus (see above) and outer walls roughly covered by fragments of palm fibres which makes them very cryptic. They are well sealed, excepting at the upper end where a very small and narrow exit can be seen; there, the palm fibres are brought together in such a way as to permit expansion by the pupa, pushing out head first, when leaving the cocoon on its way outside the palm, prior to adult emergence. After adult emergence, the cocoon keeps its former shape and volume and, should the pupal exuvia not be partly anchored on it, it is difficult to tell at first sight whether it is a live or empty one.

The cocoons are fusiform with an average length of 5.8 cm (range: 7.4–5.2 cm). Because the spindle is not symmetrical (is flatter on one of its sides), there is a widest and a shortest width: widest average width 1.9 cm (range: 2.8–1.6 cm); shortest average width 1.7 cm (range: 2.0–1.3 cm). Sample size: $n = 18$.

Historically, the first reference to the cocoon of *P. archon* was that of OBERTHÜR (1914), although referring to *josepha* (*archon*'s synonym), as follows: "Ces cocons [three brought by Monsieur PETIT from Paysandú (Uruguay)] sont grands et formés d'un tissu végétal très serré de fibres fines et dures, ayant une apparence de chien-dent." OBERTHÜR did not figure these cocoons. Later, HOULBERT (1918) complemented the description of these same three cocoons as follows: "Ces cocons n'ont pas moins de six centimètres de longueur; ils sont formés de fibres brunâtres grossièrement entrecroisées et collées entre elles, surtout à l'intérieur, à l'aide d'un mucus qui durcit fortement à l'air. Les parois chitineuses des chrysalides ont probablement été extraites après l'éclosion; en tout cas nous n'en avons trouvé aucune trace à l'intérieur des cocons." They were figured by him together in life size in an excellent photograph (HOULBERT 1918: 314, fig. 97bis).

BOURQUIN (1933) figured quite nicely and for the first time together (Fig. 12) the different life stages of *P.*



Fig. 12: Plate XXXII, reproduced from BOURQUIN (1933), depicting the life history of *P. archon*.

archon (only the last instar concerning the larva). This included one cocoon placed on the leaf axilla of a palm with a protruding pupa.

The pupal stage

The pupal stage begins when the last larval moult to pupa occurs, which happens inside the cocoon, and ends when the adult emerges, i.e. when the moth comes out from the pupal case. In fact, it is the moth (as pharate adult) inside the pupal case who, at the completion of metamorphosis, pushes the "pupa" outside the cocoon, but for practical reasons the stage will be taken as indicated.

Immediately after pupation, the pupa is pale yellowish. Later, darkening and hardening of the pupal cuticle occurs, until reaching, after about two days, a beautiful reddish brown colour (Fig. 13); this condition will remain unchanged until adult emergence.

The length of the pupal stage is also influenced by temperature, although much less than that of the prepupal stage. The values that follow refer to the pupal stage proper, i.e. they do not take into account the time spent inside the cocoon by the prepupal larva (the time corres-

ponding to phase (c) as described above). To determine such a duration, several cocoons with known history were tagged, numbered and kept in individual boxes; a cleave was then carefully cut on the cocoon walls, so that it was possible to make a daily observation inside them and check with precision when the final moult to pupa occurred, and then just counting the days until the adults emerged. This was carried out in 2003.

The results were as follows. *P. archon* pupae formed in the second half of March took an average of 66 days to complete their metamorphosis to adults ($n = 6$; sample range 63–68); those formed in the first half of April took an average of 52.3 days ($n = 6$; sample range 50–57); those formed in the first half of July took an average of 42.8 days ($n = 5$; sample range 35–49). Outside those three periods, pupae are only exceptionally formed (see life cycle below). The statement by DRESCHER & JAUBERT (2003) that the pupa of *P. archon* stays in the cocoon for a month before becoming an imago is a simplification.

The maximum/minimum temperature and relative humidity fluctuations that *P. archon* larvae/pupae underwent in the lab (from 14. III. 2003 to 18. VIII. 2003) are shown in Graph 1 (the values were recorded daily between 9 and 10 h only).

Interestingly, pupae formed in the second half of March transformed into adults 14 days later than those formed in the first half of April, so that both groups yielded adults at about the same time, indicating that some kind of synchronization (most likely driven by temperature) is in effect.

It was also noticed that pupae of *P. archon* (as it is common in most insects) react to unexpectedly low temperatures by slowing down or halting their transformation into adults. They do so as long as this abnormal situation is not long lasting and then, as soon as the “normal” temperatures return, continue their transformation. Once, in late May, we refrigerated (at 5.2–7.8 °C), for 11 consecutive days, 20 cocoons containing pupae we expected to become adults soon. After this short period, they were brought back to the current lab temperature (25 °C by then), where they all recovered well and successfully completed their metamorphosis into adults.

Data on pupal stage length for Neotropical castniids other than *P. archon* are summarized in Table 5. They refer to the pupal stage proper, i.e. they do not take into account the time spent inside the cocoon by the prepupal larva, excepting the case of SKINNER (1930) where this is not clear and most likely he meant time spent between cocoon completion and adult emergence. However, as seen above, in the Neotropics, the time spent by the prepupal larva inside the cocoon before pupating is very short (maximum 6 days, often shorter).

According to these data, it seems that, in Mediterranean Europe, *P. archon* pupal stage lasts in spring about one month longer than that of other known Neotropical castniids (range being 50 to 68 days in *P. archon*), whereas in

Table 5: Original data on pupal stage length for Neotropical castniids other than *P. archon*

Castniidae species	Pupal stage length (in d)	Source
<i>Telchin licus</i>	33–38 d	QUELCH (1910)
	30–45 d	SKINNER (1930)
	45 d	RISCO (1978)
	35–45 d	ESQUIVEL (1981)
<i>Castniomera atymnius</i>	26–35 d, mean 32 d	SALT (1929)
	20–26 d	GALLEG0 (1940)
	29–34 d for both sexes, mean 31.35 d ($n = 23$)	LARA (1964)
<i>Eupalamides cyparissias</i>	mean 30 d	KORYTKOWSKI & RUIZ (1980)

summer it gets closer to those values (range being 35 to 49 days in *P. archon*). Pupal stage length of *P. archon* in the Neotropics has thus far never been reported.

A side trial was carried out to assess the whole duration of the period that goes from the larva initiating the spinning of the cocoon until adult emergence. Note this period is the sum of phases (b) and (c) of the prepupal stage plus the full pupal stage as described above. Two groups of larvae were chosen, those that initiated the spinning of the cocoon between 22 and 26 March 2003 ($n = 10$) and those that did so between 23 June and 2 July 2003 ($n = 6$). The spring group took an average of 76.8 days (sample range: 72–85 d); the summer group did so in 52.3 days (sample range: 43–62 d). Temperature and relative humidity fluctuations underwent in the lab by those larvae/pupae were the same as in Graph 1. We noticed in specimens kept outdoors within big mesh cages that their developmental times also fell within the limits mentioned above. In addition to that, three larvae which initiated the spinning of the cocoon between 9 and 28 December 2000, obviously in the lab, and kept at a constant temperature of 22 °C, yielded the adult 58.3 days later (sample range: 56–63 d). All this means that, within some limits, the duration of this period (as well as that of the pupal stage) is clearly dependent on temperature and therefore predictable. This predictability can be used for designing pest control strategies.

Most of the abdominal segments of the pupa are furnished dorsally with transversal rows of short spines pointing backwards (Fig. 14). When ready to leave the cocoon, prior to adult emergence, the pupa lifts itself up by means of these spines and considerable mobility of the abdomen (which moves in a rotating manner), pushing against the fibres placed at the tapering top of the cocoon, loosening them and so exiting from the cocoon. If the cocoon is placed in such a way that its top just reaches the palm surface (the most common situation), when the pupa is about two thirds protruding from the cocoon, the adult starts to emerge; in such a case the pupal exuviae will be found anchored in the cocoon. How-

ever, should the cocoon be located a bit more inside the palm, the pupa comes out from it completely and then moves along the passage previously built by the larva towards the exit hole, where adult emergence will take place; in such a case, the pupal exuviae will be found either anchored in the exit hole, more or less half protruding (Fig. 15), or free on the ground just below it. This last case provides an answer to HOULBERT's (1918) amazement at the absence of pupal exuviae inside the three cocoons he analyzed from the Oberthür's collection (see above). Very similar observations to ours were reported in other Neotropical castniids by SALT (1929), LARA (1964), SKINNER (1930), ESQUIVEL (1981) and KORYTKOWSKI & RUIZ (1980). BOURQUIN's (1933) comment that the pupa produces secretions to soften the palm cellulose fibres to help itself to exit is not correct.

The adult stage

Morphology and sexual dimorphism

P. archon adults have greenish brown forewings, whereas the hindwings are orange, with a wide transverse black band containing five or six white cells. Their antennae are clubbed. Specimens reared from larvae in Catalonia showed the following wingspan:

♂♂: mean 7.48 cm (n = 18; range 8.6 cm–6.2 cm)

♀♀: mean 8.62 cm (n = 22; range 9.8 cm–6.8 cm).

There is a subtle sexual dimorphism. ♀♀ bear a long telescopic ovipositor (1.5–2 cm long when fully exerted), which is easily seen when gently pressing their abdomen (Fig. 16), their wing-coupling is mediated through six to nine long and fine frenular bristles (♂♂ have only one long and stout frenular bristle), the dorsal part of their abdomen clearly shows six anatomical segments (as opposed to seven in ♂♂) and are generally bigger than ♂♂.

Both sexes generally bear a light grey teardrop-shaped stigma on the forewings, which occurs somewhat more often in ♀♀; however, those last two characters (size and presence of stigma) cannot be used for sexing with certainty. Good colour illustrations of the adults can be found in OBERTHÜR (1914), SARTO I MONTEYS (2002), SARTO I MONTEYS & AGUILAR (2003) and DRESCHER & JAUBERT (2003). HOULBERT (1918) and MILLER (1986) contributed further morphological details, and the latter also figured and described for the first time the ♂ and ♀ genitalia as well as the labial palpus and the wing venation.

Sex ratio and adult life span

From 226 *P. archon* adults obtained from cocoons collected in the wild in 2004, 103 (45.58 %) were ♂♂ and 123 (54.42 %) ♀♀, therefore ♀♀ occurred slightly more abundantly than ♂♂, in the ratio of (♂♂:♀♀ =) 1:1.19. In other Neotropical castniids studied, the sex ratio seems to clearly favour the ♂ sex. Indeed, in *C. atymnius*, LARA (1964) reported a sex ratio of 1.53:1 (n = 48) whereas

KORYTKOWSKI & RUIZ (1980) found this was 3:1 in *E. cyparissias* (sample size not indicated).

The life span of some captive *P. archon* specimens was checked; they were kept singly in 50 cm × 33 cm × 24 cm mesh-roofed insectaries, and never fed. The ♀♀ lived an average of 14.1 d (n = 9; sample range 7–25 d) whereas the ♂♂ lived 23.8 d (n = 6; sample range: 18–37 d). Therefore, ♂ life span seems to be about 70 % longer than that of the ♀. In the ♂ that lived 37 days, it was noticed that, when being already 25 days old, it displayed a very energetic and powerful flight towards the sunlight trying to escape the insectary, which ceased when the latter was moved to a darker area.

The life span of *P. archon* in the wild is unknown, although most likely it will fall shorter than that found in captivity. In *C. atymnius*, adult life span extends from 3 to 10 days, with a mean of 6.7 d (LARA 1964); in *T. licus*, QUELCH (1910) and RISCO (1978) report a maximum of 12 d in captivity whereas ESQUIVEL (1981) reports 10–15 d; in *E. cyparissias*, KORYTKOWSKI & RUIZ (1980) report 12–13 d for the ♂♂ and 15–18 d for the ♀♀.

We also noticed that the adult life span could be significantly extended if the specimens were kept refrigerated. The moderate cold (6–7° C in the refrigerator used) kept the specimens fully motionless. Once, three newly emerged adults (2 ♂♂, 1 ♀) were immediately placed in the refrigerator and kept there until they died. In these conditions the ♀ lived 39 days, whereas the two ♂♂ lived 47 and 52 days. The latter ♂ was shortly taken from the refrigerator 36 days after it had been placed there and (at lab temperature, 22° C) still showed a very energetic drive; the same was done to the other ♂, in this case 29 d after its refrigeration, and showed the same energetic drive; however, the ♀ which was also shortly taken from the refrigerator 33 d after its refrigeration, looked very weak, and died 6 d later.

Adult behaviour

There are no specific records in the Neotropics concerning the behaviour of *P. archon* adults. However, some data exist on other Neotropical castniids. SEITZ (in SEITZ & STRAND 1913), who had extensively watched the behaviour of these moths in the wild and contributed a charming introduction to them in his monumental "The American Bombyces & Sphinges", provided some interesting observations, although some of them were certainly far-fetched and literary (see below). These, as well as those from later authors, will be commented on in the specific sections that follow.

Adult emergence and daily flight period

The physical process of adult emergence in a Neotropical castniid (*C. atymnius*) was thoroughly reported by LARA (1964) and this is indeed very similar to that of *P. archon*.

The newly emerged *P. archon* adult excretes its dark brown meconium while climbing up along any availa-

ble vertical surface, and rests to expand and harden its wings. While this process occurs, the specimens hold their wings straight up, then gradually, as wing veins harden, the wings adopt the common noctuid position. About 1–2 h after emergence, the adult is ready to fly. The time of the day when adult emergences occur is quite ample. We have observed that emergences may begin at night (around 22:00 h and later), so that specimens are ready to fly early in the morning; however, most occur in the morning, between 10:00 and 13:00 h. Emergences are extremely rare between 13:00 and 22:00 h. DRESCHER & JAUBERT (2003) report that in the laboratory, adult emergences occur early in the morning, generally before 8:00 h.

P. archon adults are day flying insects. As soon as they are ready to fly, they do so energetically (especially the ♂♂) towards the sunlight coming through the lab windows. Because of this and to minimize damage of the captive specimens, insectaries had to be moved to shady rooms. Also, we noticed that specimens kept under laboratory conditions remained inactive when cloudy or rainy conditions prevailed outdoors. We have not set exact bounds to the daily flight period in the wild, although adults were seen flying between 12:30 and 17:00 h; a copula was observed at 13:00 h. DRESCHER & JAUBERT (2003), using insect-proof tents, reported their peak of activity as being between 11:00 and 17:00 h.

SEITZ (1913), referring to Neotropical castniids in general, said they rarely start flying before 10:00 h, when the tropical sun is already strong. These observations match those of MILLER (1986), who visited eight sites in Peru and Brazil with the purpose of studying the behaviour of Neotropical castniids in their natural habitats (and sighted up to 11 species); collectively, she reported daily flight periods comprised between 9:30 and 15:00 h (excluding *E. cyparissias* which is crepuscular, see below).

LARA (1964) reported for *C. atymnius* that, whether in the field or lab, in sunny days, the moths started activity around 8:30, becoming very active between 9:00 and 10:00 h; this activity slowed down at noon and increased again right after, continuing for about two hours, and ceasing after 16:00 h. SALT (1929) added that, although diurnal and usually seen on the wing on bright days between 8:30 and 11:00 h, *C. atymnius* is a lover of shade rather than sunlight and enjoys being within the shady rows of the banana plantations. For *T. licus*, MILLER (1986) reported a daily flight period of ca. 11:30 to 15:00 h, although indicated this was affected by the morning and late evening rains.

However, *E. cyparissias* shows crepuscular fly habits; it flies in the tropical twilights, i.e. from 5:30 to 6:00 and again from 18:00 to 18:30 h (KORYTKOWSKI & RUIZ 1980); within these periods its flight is swift and synchronized, turning rather slow and clumsy in the dark of the night or in bright sunlight. MILLER (1986) reported a crepuscular flight from 17:15 to 18:45 h.

Adult feeding

Neither DRESCHER & JAUBERT (2003) nor we have ever seen *P. archon* adults feeding in the wild. In captivity, up to four ♀♀ and two ♂♂ were kept and offered fresh honey-in-water solution, on which they always refused to feed, despite being sometimes even forced to touch it with their well-developed proboscis.

In other castniids, observations seem to be confusing. SEITZ (1913) stated (referring to Neotropical castniids in general): “Les Castnies ne commencent guère à voltiger avant 10 heures, quand le soleil des tropiques chauffe déjà fortement, et cherchent de préférence leur nourriture sur les fleurs d’arbre ... elles visitent de préférence les fleurs blanches ou d’un rouge vif ... la *Castnia* court, bourdonne et saute de fleur en fleur, enfonçant son puissant suçoir avec une grande rapidité dans une corolle après l’autre. Elles sont admirablement organisées pour transporter le pollen, et malgré les écailles lisses, quoique très grossières, ce n’est pas rare de rencontrer des exemplaires tout à fait saupoudrés de pollen; chaque insecte porte ainsi la couleur de sa fleur favorite ... Dans la plupart des cas la capture des Castnies comme papillon est également assez difficile; c’est sur les fleurs qu’on la prend le plus facilement. Sur des arbres en fleurs j’ai pris assez souvent de bons exemplaires de *C. pallasia* [*Imara pallasia* (ESCHSCHOLTZ, 1821)] et quelques *decussata* [*Geyeria decussata* (GODART [1824])].” ROMERO (1997) saw, in Venezuela, adults of *Haemonides cronis* (CRAMER, [1775]) nectaring on flowers of the median sized tree *Warscewiczia* sp. (Rubiaceae). He also collected a ♀ of *Athis palatinus* (CRAMER, 1777) (of ssp. *axaquia* J. GONZÁLEZ & F. FERNÁNDEZ, 1992) on the same flowers; although this specimen was not observed actually nectaring, it is likely it was there for this reason (J. GONZÁLEZ, pers. comm.). COMMON (1990), referring to the genus *Synemon* (Australian castniids), reported that adults had occasionally been observed feeding at flowers.

On the other hand, JÖRGENSEN (1930), who contributed valuable information on the distribution and biology of all known Castniidae of Argentina and Paraguay, stated that “despite having seen hundreds of specimens I have never seen them visiting flowers [for nectaring]”. SKINNER (1930), referring to *T. licus*, reported: “This moth does not appear to feed as a rule, but specimens have been seen feeding on flowers of the ‘Railway Daisy’ *Bidens pilosus* [Asteraceae]; these were invariably very dilapidated specimens with wings much broken by flying through the cane trash. It is probable that the business of egg-laying being over, they had a little leisure in which to feed, but that, as a rule, they die without feeding. They are very fond of water, however, and spend a lot of time clinging to the moist and shady sides of ravines and drains.” J. GONZÁLEZ (pers. comm.) saw a ♂ *T. licus* sucking fluid from the tip of a banana fruit previously pecked by a bird. ESQUIVEL (1981), also referring to *Telchin licus*, stated: “An important finding about the biology of the adult is that it does not feed at all during this stage.” SALT (1929)

and LARA (1964), who thoroughly studied the behaviour of *Castniomera atymnius*, made no comments on adult feeding (as if they had not seen the moths feeding at all). KORYTKOWSKI & RUIZ (1980) never saw adults of *E. cyparissias* visiting flowers, although occasionally some were observed on the wounds produced by the cutting of fruit bunches or leaf rachises after harvesting or pruning the oil palm. J. GONZÁLEZ (pers. comm.) saw a newly emerged *Eupalamides guyanensis* (HOULBERT, 1917) ♂ introducing its proboscis into the crack of a fresh *Cocos nucifera* palm trunk chunk (on which the larva had been reared); he also saw a very worn-out ♂ of *Castnia invaria penelope* SCHAUFUSS, 1870, on a pineapple plantation, sucking the fermented juice present on the exposed cut surface of a pineapple fruit. MILLER (1986), who observed up to 11 Neotropical species in their natural habitats (see above), never reported them nectaring. EDWARDS et al. (1999) made no comments on adult feeding behaviour of castniids.

Territoriality and perching behaviour of ♂♂

P. archon ♂♂ are very territorial and fly in hot, sunny weather. Their flight is very powerful, rapid and darting (an estimation would be 20 m/s), being able to hover for a few seconds; the flight path is generally straight although right/left shifts are frequent and the moth can be seen balancing its body accordingly. They fly over and over rather small areas, returning to the same perching places. Their orientation skills are extraordinary, being capable of flying hundreds of meters, disappearing from human sight for several minutes and coming back exactly to the same palm leaf they had taken off from.

♂♂ usually perch on palm leaves or cut rachises around the palm trunk close to the crown. When they see a flying object close to their own size, not necessarily conspecific, they immediately take off towards it. When reaching it, if not conspecific, they quickly fly back to the perching spot. However, if conspecific, a pursuit begins. ♂♂ follow either other ♂♂ or ♀♀; groups of generally two adults can be seen together “pursuing” each other. However, should such flying pair cross the territory of another ♂, this third one would immediately join the pursuit so that the flying group would now be of three, or even four, if a fourth ♂ joins. While the pursuit is on, they keep a distance of about 10–100 cm among them; no collisions have been observed. It looks like as if they wanted to show to each other their flying power and skill. This intense flight, though, is short-lived, as they are continuously changing direction, and even also changing pursuer; it reaches a height of about two meters above the palm crowns, generally not higher, maybe because they do not like to get too far away from the palms or simply because they feel less secure in the open air. These pursuits seemed to be somewhat different should the intruder be a ♀; in such cases, the pursuing flight looked slower than that described above (see below). When one of the ♂♂ abandons the pursuit, whatever the reason might be, it flies back, now calmly and slowly, on a low flight (about 1.5 m above the

ground, underneath the leaves of the row-lined palms), to the former perching spot, where it rests waiting for another intruder to come by.

DRESCHER & JAUBERT (2003), using insect-proof tents, had already reported a territorial behaviour in *P. archon* ♂♂, although tent dimensions prevented a fully natural observation of such behaviour, so that, for example, the darting, rapid flights were not mentioned.

The territoriality and perching behaviour shown by *P. archon* ♂♂ seems to be very similar to that mentioned in other Neotropical castniids by authors like SEITZ (1913), SALT (1929), LARA (1964), MILLER (1986) and ROMERO (1998).

Mating behaviour

When the intruder entering a territory patrolled by a *P. archon* ♂ is a conspecific ♀, the pursuit that follows is slower and lower than that described above. The pair flies along the palm rows, close to each other (about 20 cm), at heights lower than 2 m above the ground and very close to the palm crowns (in the studied plot). Then, they alight, led by the ♀, on a leaf or on the crown of a palm. The ♀ walks shortly until reaching a spot where it can rest comfortably, folding its wings in the common noctuid position. The ♂, who has been closely following the ♀'s movements a few centimeters behind, moves side by side to the ♀, approaching along her right side and, by bending laterally its abdomen towards the tip of that of the ♀, the copula is accomplished. In the case observed, copulation lasted for about 37 min, after which the ♂ calmly took off; the ♀ stayed but fled away when we tried to collect it (Fig. 17a, b).

DRESCHER & JAUBERT (2003), using insect-proof tents, also observed a mating of *P. archon*. However, they reported the copula as lasting only 1–2 min. This is a very short time for a copula in castniids (see below) and most likely was terminated by an accidental interruption. They also said that ♂♂ are the ones who attract the ♀♀ and not the opposite. However, our field observations do not support this. ♂♂ and ♀♀ occur together within palm plots where the larvae completed their development to adults. ♀♀ simply move around within these areas until they are spotted by a patrolling ♂ as explained above, in much the same way as butterflies do. The fact that electroantennograms carried out using ♀ ovipositor (hexane) extracts, triggered a positive and significant response in ♂ antennae, seems to indicate that *P. archon* has at least a ♀-released short-range pheromone for conspecific sex recognition, while ♀-released long-range pheromone, i.e. that used by other heterocerans to attract conspecific ♂♂ at longer distances, might be absent in *P. archon* and replaced by visual attraction as described above. It must be recalled that castniids are day-flying and, at least in the Neotropics, many species bear an outstanding mimetic resemblance in shapes and colours to Neotropical butterflies (MILLER 1986). As it is well known, ♀ butterflies do not release long-range pheromones to attract their

conspecific ♂♂; ♂♂ chase after them when they see them and later, at close distance, ♂ scents (from androconia scales) may help with sex recognition. If, during the course of evolution, ♀ castniids had lost the capability of producing long-range pheromones, as it seems to be the case in *P. archon* and, most likely, in other Neotropical castniids, this would be an important apomorphic trait, which will separate them further from Sesiidae and Brachodidae, the other two families in the superfamily Sesiioidea.

So far, not a single castniid pheromone is known. Only REBOUÇAS et al. (1999), working with *T. licus*, found that a hexane extract from ♀ ovipositors elicited activity from ♂♂ in a behavioural bioassay (very similar to what we experienced with *P. archon*). Analyses by gas chromatography and mass spectrometry allowed those authors to determine the major constituents present in the hexane extract as n-alkanes C_{21} to C_{30} , (Z)-9-hexadecenoic acid (C_{16}), (Z)-9-octadecenoic acid (C_{18}) and hexadecanoic acid (C_{16}). Aldehydes, alkenes and acetates were also detected in low concentrations in the extracts.

Mating of castniids in the wild seems to be rarely seen. SEITZ (1913), having never sighted a copula after extensive observation, wrongly believed this might take place in flight, like that of dragonflies. As far as we know, the first mention of a pairing in castniids, although in captivity, was that of MOSS (1945) for *Castnia invaria* WALKER, 1854 (quoted as *Castnia icarus* CRAMER). LARA (1964), in *C. atymnius*, reported that mating was observed only in the afternoon hours and on top of banana leaves; copulation lasted for an average of 30 minutes. KORYTKOWSKI & RUIZ (1980), in *E. cyparissias*, reported that mating occurs usually after the two daily flight periods (see above), mostly after the early evening one, on the apical section of a leaf; copulation is long lasting, 1–3 h, sometimes even more. COMMON & EDWARDS (1981) reported for one Australian species, *Synemon magnifica* STRAND, 1911, that mating was observed once. They explained that this occurred after a ♀ was pursued by a ♂ and landed on a dead vertical twig. After this “the ♀ remained motionless with wings folded so as to cover the twig, while the ♂ landed below and slowly walked up the twig until level with and facing the ♀”. Copulation followed and both then remained almost motionless for 3:15 h.

In order to check whether *P. archon* adults were capable of mating in captivity, trials were carried out in small insectaries and big cages. On 27. iv. 2001, a freshly emerged pair was placed in a median size insectary (50 cm × 33 cm × 24 cm, mesh-roofed); it also included a fresh palm trunk of *T. fortunei* palm (which had been the larval foodplant) and Petri dishes containing honey-in-water solution. ♂ and ♀, though, never fed, completely ignored each other, and no mating was detected. The ♀ died on 19. v. 2001. The couple stayed together for 23 d. One big wire mesh cage (1.20 m × 1.50 m × 2.10 m), containing many recently cut *T. fortunei* palm trunks bearing live cocoons, was also tried in July 2004. The cage

was set outside, under the shade of pine trees; in such more natural conditions, mating pairs (formed among specimens emerged in the cage) were regularly sighted, either on the cage walls or on the palm trunks. Some of those mated ♀♀ were set apart in small 700 ml transparent plastic cylinders kept in the laboratory and laid eggs which hatched normal larvae. A bigger mesh cage (1.85 m × 2.50 m × 2.05 m), containing four planted *T. fortunei* palms (Fig. 18), was also tried, and matings were again observed on its walls.

Also, in southeastern France, using a greenhouse, some matings were sighted (DRESCHER, pers. comm.); they took place on the upright sides of the greenhouse mesh, on which the ♀ had alighted followed by the ♂. However, despite pairings still do occur within big cages and greenhouses, it is obvious that the complex mating behaviour observed in the wild and described above, where territoriality and quick and vigorous flights are required, cannot be properly performed unless big areas are available to the moths.

Oviposition behaviour and fecundity

While *P. archon* ♂♂ are territorial and patrol their territory as explained above, ♀♀ fly freely around the palm plot, visiting palm after palm, with an irregular, low and slow flight, searching for an appropriate crown to lay their eggs. Their selection criteria for egg laying are not known. Sometimes, a ♀ lays eggs on several palms located very close to each other, whereas other times it flies tens of meters before ovipositing on another palm. Between oviposition bouts, they also normally rest in the shade, provided by palms or other neighbouring trees, for several minutes or even for hours, where they are very cryptic.

According to DRESCHER & JAUBERT (2003), *Paysandisia archon* ♀♀ offered five different palm species (in insect-proof tents), *Chamaerops humilis*, *Livistona chinensis*, *Phoenix canariensis*, *Washingtonia robusta* and *Phoenix roebelenii*, showed a clear preference for ovipositing on the latter.

When ovipositing, the ♀ tends to place itself back-facing the palm crown, so that it can see the outside while introducing more easily the ovipositor through the palm fibres for egg laying. It must be mentioned that adult vision is very good on the frontal part, whereas it is null on the back, which makes the moth more vulnerable to predation (in fact, we collected once one ♀ with our own hands, approaching it from behind).

Historically, the first mention of egg laying in *P. archon* was contributed by HOULBERT (1918), although referring to *P. josepha* (OBERTHÜR, 1914), a synonym of *P. archon* (BURMEISTER, 1880), based on the information given to him by Monsieur Joseph PETIT from Paysandú (Uruguay). M. PETIT wrongly said to HOULBERT that eggs were laid underneath the leaves of a “spiny leaved” palm. This palm, although not specified in HOULBERT’s work, was *P. canariensis* (SARTO I MONTEYS 2002).

Later, BOURQUIN (1930), most likely reporting what had been told to him by Joseph DE BOISMENU, also from Pay-sandú and nephew of Mr. Joseph PETIT (see SARTO I MONTEYS 2002 for further details), added the following: “By means of this one [referring to the ♀ ovipositor] lays its eggs inside a small hole and, it seems, always singly.” The palm species on which this egg laying took place as well as the meaning of the “small hole” were not specified in his 1930 paper.

Finally, BOURQUIN (1933, 1944) corrects and specifies the above data as follows: “The ♀ .. does not deposit the eggs on the leaves as has been written, but on the hollow that the leaf forms when leaving the trunk or, also, on the fibre web that usually covers the palm trunk at the leaf base.” These observations fully agree with ours, seen on *Trachycarpus fortunei* palms in Girona (Spain).

Indeed, most *P. archon* eggs are found within the fibre webs closest to or within the palm crowns (in *T. fortunei*, on the circular fibre bands placed immediately below the projecting leaf rachises). The eggs are not glued to the fibres, remaining loose within their thick layers; because of their location (1–2 cm inside), they are not easily seen from the outside, which might decrease predation and parasitism, and are protected against direct sunlight and rain. If those layers of fibre web holding the eggs are removed from the palm trunk and pulled apart, the eggs fall out freely.

♀♀ lay eggs (through their long extensible ovipositor) in a very quick and little noticeable way; sometimes it looks like the eggs are laid as the ♀ walks across the palm crown. Eggs are laid singly, despite, sometimes, palm fibres may contain several eggs very close to each other (Fig. 19); indeed, the same ♀ could lay several eggs on the same palm crown. DRESCHER & JAUBERT (2003) point out that eggs are laid not singly but in groups of 7 to 10, most frequently 9, which, according to these authors, would be in accordance with beads of 9 eggs found in the oviducts of dissected ♀♀ (which had been found dead). Our field data do not support this and also this arrangement (beads of 9 eggs in ♀ oviducts) could not be seen in ♀♀ dissected by us. Data brought forward in other Neotropical castniids also indicate that eggs are laid singly: at the base of the cane, between the dry trash and the stem in the Giant Cane Borer, *T. licus* (SKINNER 1930, ESQUIVEL 1981), on the palm crown (mostly on green fruit bunches) or on the axillae of leaf rachises underneath the crown in the Oil Palm Borer, *E. cyparissias* (KORYTKOWSKI & RUIZ 1980) and on or around the base of the banana plant in the Banana Stalk Borer, *C. atymnius* (GALLEGO 1940, LARA 1964).

A *P. archon* ♀, which had just mated at 13:00 h, was collected in the wild on 19. vi. 2003 and taken to the laboratory. There, it laid eggs as shown on Table 6.

Therefore, since it was collected in the wild, it lived 8 d in captivity, laying 115 eggs. 25 additional eggs were found in its abdomen by dissection (which obviously did not develop an embryo). All but two eggs laid hatched normally;

Table 6: Oviposition sequence in laboratory conditions of a just-mated, field-collected, *P. archon* ♀ (collected on 19. vi. 2003; deceased on 27. vi. 2003).

Dates	Eggs laid
20. vi. 2003	2
21.–23. vi. 2003	11
24.–25. vi. 2003	98
26.–27. vi. 2003	4 (the ♀ dies on 27. vi. 2003)
	25 found in the abdomen of the dead ♀
Sum:	140 eggs

one of the two unhatched eggs had a perfectly formed larva inside, the other did not develop an embryo. So, at least in this case, egg viability was very high, 98.26 %. In *E. cyparissias*, KORYTKOWSKI & RUIZ (1980) reported an egg viability of 80.5 %.

According to DRESCHER & JAUBERT (2003), egg laying in *P. archon* begins quite soon after mating; they reported that, at least in one case, it begun only two hours later. They found egg laying to last up to ten days after mating; one ♀ laid 110 eggs within its first two days whereas others prolonged it further. KORYTKOWSKI & RUIZ (1980) reported in *E. cyparissias* that egg laying lasted for 12–17 d, starting not before 24 h after the copula; most of the eggs (a mean of 265 in this species) were laid during the first 5 d.

P. archon ♀♀ reared in the laboratory and kept virgin in insectaries, either laid no eggs throughout their lives or, if they did, the number was very small (less than 5). However, ♀♀ collected in the wild were caged and laid eggs which hatched normal larvae (see above). Therefore, it seems likely that ♀♀ do not normally lay eggs unless mated. Very similar observations were reported by LARA (1964) in *C. atymnius*.

We dissected 3 virgin ♀♀ which were known not to have laid a single egg. Their abdomens were filled with rosy eggs, amounting to 134, 148 and 143 respectively. The mated ♀ collected in the wild on 19. vi. 2003 (see above) amounted to 140 eggs. ♀♀ dissected by DRESCHER & JAUBERT (2003) (sample size not indicated) contained an average of 130 eggs. Therefore, although the average number of eggs a ♀ lays in the wild is not known with certainty, this will probably fall within 80–90 % of its full egg production capacity, which seems to be around 140 eggs. Compared to other heterocerans, including other castniids (see below), this is not a high fecundity.

Some data are available concerning fecundity in other Neotropical castniids. In *E. cyparissias*, KORYTKOWSKI & RUIZ (1980) indicate that ♀♀ lay from 200 to 500 eggs, with a mean of 265; they provide no data as to the eggs found in virgin ♀♀ by dissection. In dissected virgin ♀♀, QUELCH (1910) counted in *T. licus* as many as 144 eggs; beyond these coloured eggs, the ovarian tubules were constricted for many others, giving an egg capacity of more than 200. In *C. atymnius*, LARA (1964) found slightly over 270 eggs.



Plates 3 and 4: *Paysandisia archon*. **Fig. 17:** Mating pair of *P. archon*. **Fig. 17a:** The ♂ appears partially covered by the ♀. **Fig. 17b:** ♂ (on the right) leaving just after copula. **Fig. 18:** Big mesh cage, containing planted *T. fortunei* palms, used to find out whether *P. archon* adults were capable of mating in captivity as well as to monitor the larval and pupal development (along with that carried out in the lab). **Fig. 19:** Two eggs laid (loose, not glued) within the palm fibre meshes; those meshes on top of the eggs were removed. **Fig. 20:** Empty, albeit unhatched, egg of *P. archon*, most likely due to parasitism by a hymenopterous egg parasitoid or to predation by an oophagous hemipteran. **Fig. 21:** Pupal exuviae protruding from a heavily infested

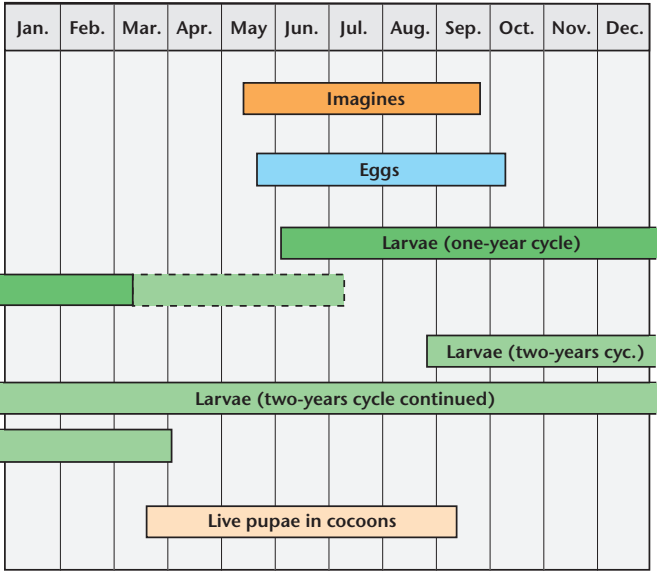
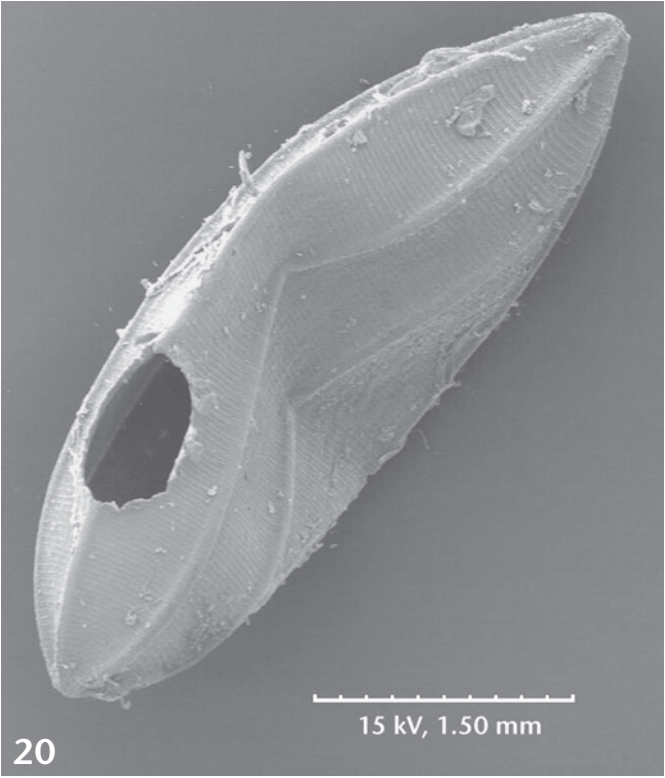


Table 7: Life cycle of *P. archon* in Mediterranean climate.



T. fortunei palm trunk. Fig. 22: Other symptoms of infestation by *P. archon* on palm trees: Fig. 22a: Presence of sawdust on the palm trunk. Fig. 22b: Presence of perforated leaves (non specific). Fig. 22c: Presence of gallery holes within the palm trunk. Fig. 22d: Abnormal development of axillary leaf buds. Fig. 22e: Deformation and abnormal twisting of palm trunks. Fig. 22f: Abnormal drying up of the palms, specially the core leaves. Fig. 23: Dead *T. fortunei* palm because of *P. archon* larval attack.

Curiously, the number of eggs actually laid in captivity by mated castniid ♀♀ seems to be low. In *T. licus*, SKINNER (1930) reported that trials carried out in Trinidad with newly mated ♀♀ indicated that some 45 eggs was the maximum laid per ♀; RIBEMBOIN (1964), in Pernambuco (Brazil), estimated this as being between 50 and 100 eggs whereas ESQUIVEL (1978) found an average of 40 eggs in Panamá. In *C. atymnius*, GALLEG0 (1940) reported that ♀♀, in Colombia, laid between 30 and 40 eggs. In *P. archon*, seven ♀♀ who had just mated (in July 2004) were set apart and kept individually in 700 ml plastic cylinders placed in the laboratory. They lived 9, 21, 8, 11, 9, 15 and 5 d and laid, through these days, 35, 68, 24, 10, 25, 49 and 6 eggs respectively, which later hatched normal larvae. We believe this poor egg laying in captivity responds simply to the fact that castniid ♀♀ are very selective about the natural locations where their eggs should be laid.

Life cycle

The life cycle of *P. archon* is not simple, especially concerning its larval stage; it is shown on Table 7 from data collected in coastal Catalonia.

P. archon adults appear in the wild in mid-May and disappear in late September, with a peak during June and July; sightings of adults in May, August and September are much rarer. Graph 3 summarizes such expected seasonality in Catalonia which does not result only from adults actually seen in the wild (only a few have actually been seen) but mostly from the actual sequence of adult emergences (through the years 2001, 2002 and 2003) obtained from a sample of 70 larvae collected in the wild (mostly in winter time), and reared to pupae in a non-heated/cooled lab (see Graph 2). Note, in Graph 2, that most adult emergences (80 %) occurred up to the first ten days of July; from the second ten days of July until late September only a few emergences occurred (20 %). Emergences occurring (in the lab) before the second ten days of May are rare and occasional and would not take place in the wild.

The fact that mid May and late September are the beginning and the end of the occurrence of *P. archon* adults in the wild is also supported by the finding in the wild of fertile eggs in early June (specifically on 4. vi. 2002) and early October (specifically on 1. x. 2002). Besides, some fresh looking pupal exuviae protruding from palm trunks found in the wild in the second half of May support such mid May beginning of adult flight. Also, on one occasion, four adults were seen flying in the wild on 5. vi. 2003; as said before, sightings are more common in later dates and until the end of July.

Live, unhatched eggs are expected to be found from late May to mid-October (see above); they appear creamy pink when freshly laid, darkening to brown as the days pass. Results concerning the duration of embryonic development can be found above. Live eggs do not overwinter.

Because the larvae do not eat the chorion after hatching, hatched eggs, which look dull white, can be found at any time within the palm fibre webs where they were laid.

The larval stage is the longest and most complex of all *P. archon* stages. It is the only one that overwinters; during winter time, nearly all larval instars can be found within the palms in the wild, including prepupal ninth instar larvae.

A first group of larvae (generally those hatched from June to August) will overwinter only once, yielding adults from mid-May to September next year, although some of these larvae will exceptionally overwinter twice (meaning the group B of larvae as described in the section "Unusual lethargic periods" above). This situation determines a one-year cycle for the species; the larval stage lasting ca. 10.5 months. Because, according to the adult seasonality mentioned above (Graph 3), most eggs will be laid between late May and the first ten days of August, it can be concluded that the one-year cycle is the one undergone by the majority of the *P. archon* population in the wild. For instance, two larvae reared in the lab from hatching to adult emergence did so in 360 (a) and 368 (b) days (a: hatching 9. viii. 2002, adult 4. viii. 2003, larval stage lasting 321 days; b: hatching 11. viii. 2002, adult 14. viii. 2003, larval stage lasting 319 days). The lab was neither heated nor cooled in cold/hot weather respectively, temperatures ranging between 12° C and 30° C; Graph 1 shows those exact values from 14. iii. to 18. viii. 2003. DRESCHER & JAUBERT (2003) reared in the lab (temperature 25° C ± 2° C) one larva which had hatched in July 2001; in these highly unnatural conditions (the temperature was kept more or less constant over the whole development) it reached the adult stage in April 2002, therefore ca. 304 days later. It is likely this is the shortest possible developmental time, from hatching to adult emergence, for *P. archon*.

A second group of larvae (generally those hatched from September to mid October) will overwinter twice, yielding adults from mid May to July of the second year. This determines an almost two-year cycle for the species; the larval stage lasting ca. 18.5 months.

Live cocoons (i.e. including live pupae) can be found from mid-March to mid-September. Empty cocoons can be found at any time, as they remained on the palms after adult emergence; they keep their former shape and volume, being obviously much lighter in weight than live ones.

In summary, the *P. archon* life cycle in Catalonia comprises, from egg to egg, an average of 389 days (i.e. 12.8 months) in specimens having a one-year cycle and an average of 673 days (i.e. 22.1 months) in specimens having a two-year cycle.

As for the total length of the life cycle in other Neotropical castniids, SKINNER (1930), in *T. licus*, indicated that this would appear to vary between four and six months, although admitting it was never possible to rear any from

the egg to the adult stage; in northeastern Brazil, RISCO (1978) reported 177 days (5.8 months). LARA (1964), in *C. atymnius*, found it was from 102.9 days (3.4 months) to 148.2 days (4.9 months), with a mean of 122.97 days (4 months). KORYTKOWSKI & RUIZ (1980), in *E. cyparissias*, found it was from 217 days (7.1 months) to 493 days (16.2 months), with a mean of 314 days (10.3 months). MILLER (1986), referring to Neotropical Castniidae in general, reported a life cycle of 6–9 months, and used this characteristic as one of those differing with the Australian Castniidae, the latter having a two-year cycle. Needless to say, the above mentioned data do not support MILLER's conclusion, which resulted from incomplete, premature and incorrect data.

In spite of the fact that the life cycle of *P. archon* is so far not known in the Neotropics (MILLER 1986), Mr. A. E. VARGA presented us some unpublished data concerning the occurrence of the adult stage in the province of Buenos Aires (Argentina). Adults begin appearing in early November and can be seen until early May, i.e. from mid-spring to mid-autumn in the Southern Hemisphere, in what seems to be one generation per year. This is indeed quite similar to the occurrence of the adult stage in coastal Catalonia, in the Northern Hemisphere (see above), although in this Mediterranean region adults become scarce from mid-summer and virtually disappear by the end of this season. It seems, therefore, that *P. archon* has been able to adjust its life cycle quite successfully to the new environment in the Mediterranean. In fact, *P. archon* is amongst those castniid species occurring farthest to the south in the Neotropics, virtually at the southern border for the American Castniidae as a whole. Graph 4 shows the average temperature and rainfall in the cities of Girona (Catalonia, Spain) and Buenos Aires (Argentina), both in areas where *P. archon* is established; to make it comparable, months have been aligned according to the meteorological season in each area, starting with winter and ending with autumn. Note the striking similarity of the temperature line in both areas, being Buenos Aires only slightly warmer, as an average, than Girona.

Interestingly, KORYTKOWSKI & RUIZ (1980) estimated the following seasonality for *E. cyparissias*, another palm borer, in the Department of San Martín, Peru, a region located close to and south of the Equator. The adults and, following closely, the eggs would occur between June and August; earlier instar larvae between mid-June and October; median instar larvae between September and January; later instar larvae between December and March; prepupal larvae between mid-March and April; pupae in May. This life cycle implies one generation per year and has many similarities with the one-year cycle shown by *P. archon* (see Table 7).

Larval foodplants

P. archon larvae seem to be specialized feeders on Arecaeae (palm trees) as all reported foodplants fall within this

monocotyledonous family; however, within it, the larvae are very catholic feeders, given the variety of genera they attack (see below). It is worth noting that once we offered a larva, who had been starving for three days, the fruit top (including the leafy part) of the commercial pineapple (*Ananas comosus*, Bromeliaceae) and it fed on it and seemed to recover. MILLER (1986) points out that other Neotropical castniids, with known foodplants other than pineapple, can also feed for a short period on this bromeliad, especially first instar larvae, although all attempts made to rear those larvae on it were unsuccessful.

So far, in the Neotropics, the following palm species have been reported as foodplants for *P. archon* (all data based on larvae/cocoons actually found on the palms): At Paysandú (western Uruguay) on *Phoenix canariensis* (HOULBERT 1918), *Phoenix canariensis* and *Trithrinax campestris* (BOURQUIN 1930), *Phoenix canariensis*, *Trithrinax campestris*, *Butia yatay*, *Chamaerops humilis* and *Livistona chinensis* (the latter quoted as "Latantias") (BOURQUIN 1933). In the Brazilian state of Rio Grande do Sul, DE BIEZANKO (1961) reported *Syagrus romanzoffiana*, *P. canariensis* and *L. chinensis*; the same three palms were also mentioned by RUFFINELLI (1967) from neighbouring Uruguay, although most likely he just used DE BIEZANKO's data. In northern Argentina, VARGA (pers. comm.) indicated that, in the Province of Buenos Aires, at least the following palm species are affected: *P. canariensis*, *T. campestris*, *Butia yatay* (the most affected) and *Butia capitata* (the least affected).

In Europe, it has been found so far on the following palm species (arranged by countries):

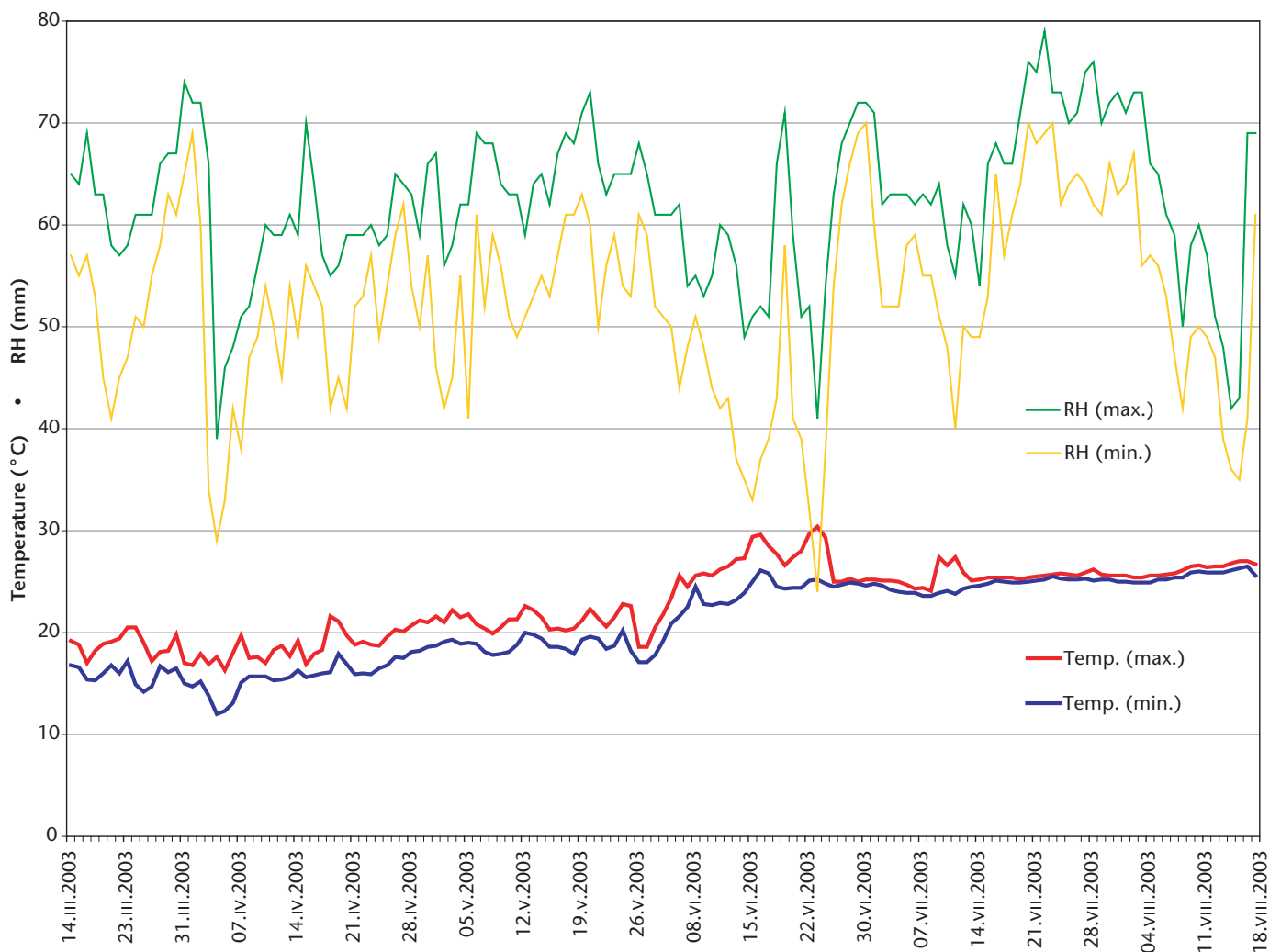
Spain:

Catalonia: *Trachycarpus fortunei*, *Chamaerops humilis*, *Phoenix canariensis*, *Phoenix roebelenii*, *Washingtonia filifera*, *Trithrinax campestris* and *Sabal* sp. (possibly *S. minor*). [Data provided by the Servei de Sanitat Vegetal, Generalitat de Catalunya.]

Comunidad Valenciana: *Trachycarpus fortunei*, *Chamaerops humilis*, *Phoenix canariensis*, *P. reclinata*, *P. roebelenii*, *Syagrus romanzoffiana*, *Washingtonia filifera*, *W. robusta*, *Brahea armata* and *Livistona* sp. (ANONYMOUS 2003).

Note: Despite the fact that the presence of this pest in this Community was only officially declared in May 2003, according to J. F. BALLESTER-OLMOS (pers. comm.), from the Instituto Valenciano de Investigaciones Agrarias, he had already found larvae of *P. archon* in the second half of the 1990s (1996–1999), in some localities within Valencia Province, especially in Bétera and Albal, damaging considerably palm nurseries of *Phoenix canariensis* and *Chamaerops humilis*. However, by then, the larva was thought to belong to the Noctuidae family and could not be identified; the presence of such an unknown "noctuid" larva was reported by BALLESTER-OLMOS (2000).

Balearic Islands: In Pollença, north of Mallorca, some stands of native *Chamaerops humilis* were found to be attacked in September 2003 (Joan COLL, pers. comm. Secció de Sanitat Vegetal, Govern de les Illes Balears).



Graph 1: Temperature and relative humidity (RH) fluctuations, measured daily, in the laboratory where *P. archon* larvae/pupae were reared (14. III.–18. VIII. 2003).

France:

Southeastern France. DRESCHER & JAUBERT (2003) listed 21 palm species, belonging to 9 genera, on which *P. archon* damage had been noticed: *Brahea armata*, *B. edulis*, *Butia capitata*, *Chamaerops humilis*, *Livistona australis*, *L. chinensis*, *L. decipiens*, *L. saribus*, *Phoenix canariensis*, *P. dactylifera*, *P. reclinata*, *P. roebelenii*, *P. sylvestris*, *Sabal mexicana*, *S. minor*, *S. palmetto*, *Trachycarpus fortunei*, *T. wagnerianus*, *Trithrinax campestris*, *Washingtonia filifera* and *W. robusta*.

Italy:

Campania: ESPINOSA et al. (2003) reported the discovery, in November 2002, in Salerno, of three adults (two in copula) of *P. archon*, although the host palm tree for the larvae was unknown.

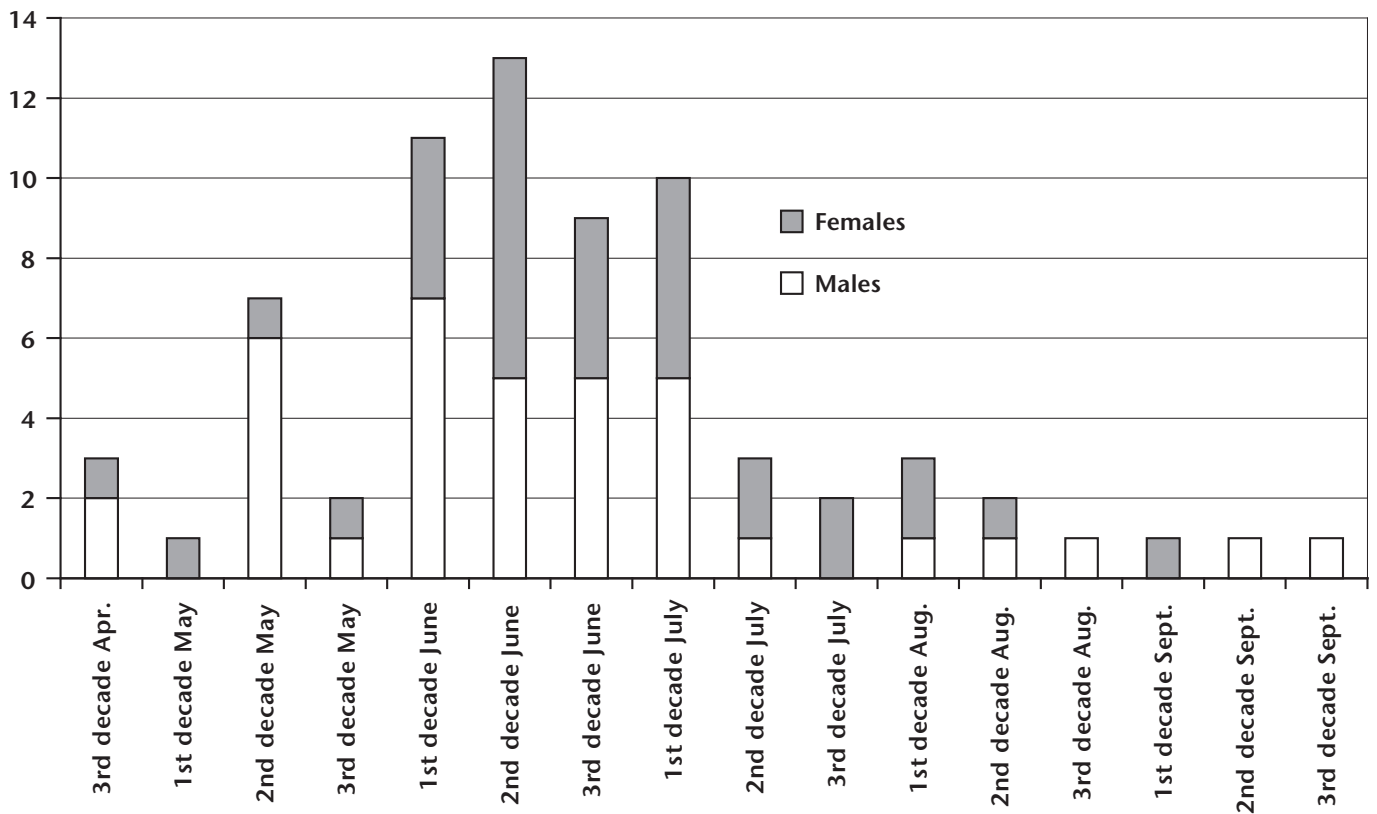
Marche: In autumn 2003, a well-established population of *P. archon* was found in several nurseries in southern Marche, mostly around the district of Grottammare (Ascoli Piceno Province). Larvae were found attacking *Chamaerops humilis*, *Phoenix canariensis*, *Trachycarpus fortunei* and *Washingtonia* sp. Those nurseries suffered serious damage and many palms were found dead (sometimes up to 90%). It seems *archon* was introduced in this

area at least 4–5 years ago, most likely from infested palms coming from Argentina and Spain (N. ISIDORO pers. comm.).

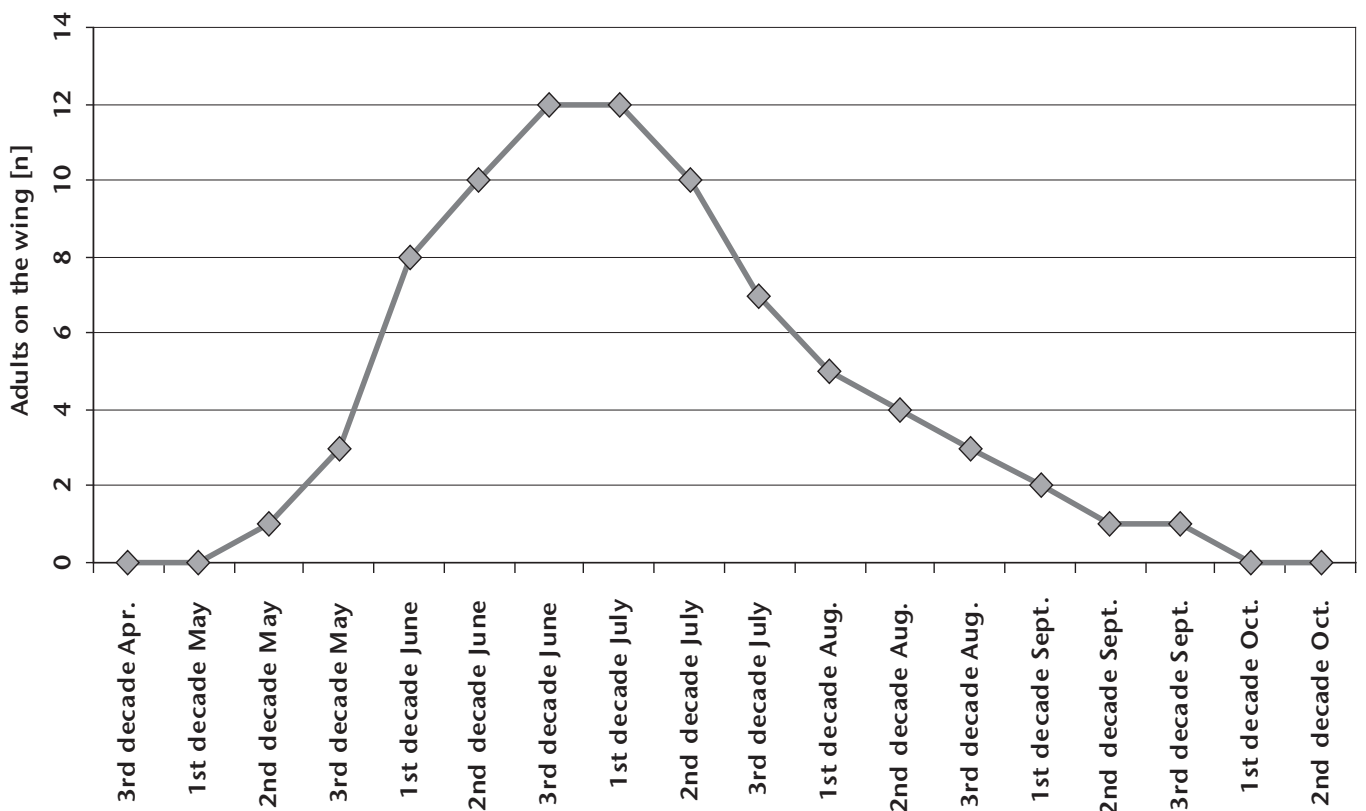
Pest status of *P. archon* and other Neotropical castniids

The first indication that larvae of *P. archon* (quoted as *josepha*) might cause damage to palm trees (specifically to *P. canariensis*) was given by HOULBERT (1918) (see above).

BOURQUIN (1933) reported the following, concerning the pest status of *P. archon* (translated from Spanish): “In 1913 *Castnia archon* was rare, but in 1927–1928 it has become a true pest, to the extent that the larvae killed a big quantity of exotic palms, such as *Latantias* [most likely referring to *Livistona chinensis*], *Chamaerops*, *Phoenix canariensis*, some of them being 80 cm in diameter. As an example it can be mentioned the case of the garden of the Hospital of Paysandú, where 15 out of 20 palms died, more than 30 years old. Native palms, such as the Coco Yatay, *Martius* sp. [*Butia yatay*] and the Caranday, *Trithrinax campestris*, do not seem to suffer much from the larvae of this moth, although are very much bored



Graph 2: Adult emergences of *P. archon* (2001–2003) (from 70 larvae reared in captivity).



Graph 3: Seasonality of *P. archon* adults in Catalonia (Spain).

by them. The following year the pest disappeared and at present [= September 1932] is rare again.”

LEPESME (1947) quoted three castniids as possible palm pests: *E. cyparissias*, *T. licus* and *P. archon*. As to *archon*, no further details followed those already contributed by BOURQUIN (1933).

MILLER (1987) reports that most Castniidae are economically unimportant with the exception of three genera, *Castniomera* (with *C. atymnius humboldti* (BOISDUVAL [1875]) on bananas), *Telchin* (with *T. licus* on sugarcane) and *Eupalamides* (with *E. cyparissias* on african oil palm); she makes no reference to *P. archon* as a palm pest, alt-

though in a previous work (MILLER 1986) she had quoted BOURQUIN's (1933) comments on the damage its larvae caused to palms in 1927–1928 in Paysandú, as reported above. OSORIO ROJAS (1972) though, had mentioned *Castnia invaria* WALKER, 1854 (quoted as *Castnia icarus* CRAMER) as an insect of economic importance on commercial pineapple (*Ananas comosus*, Bromeliaceae) in the central-western region of Venezuela; the larvae formed large tunnels in the centre of pineapple plants and at times fed on the flowers or young fruits; although the species did not seem to be abundant, it caused serious damage since its attacks resulted in the production of numerous small subsidiary plants and a consequent loss of yield. Finally, ZHANG (1994), when indexing all known economically important Lepidoptera, does mention (with some confusion because of several synonymic names) the last four species (not *P. archon*) and adds that the Brazilian *Athis therapon* (KOLLAR, 1839) is a minor pest of Orchidaceae, which was once introduced to New Jersey (USA).

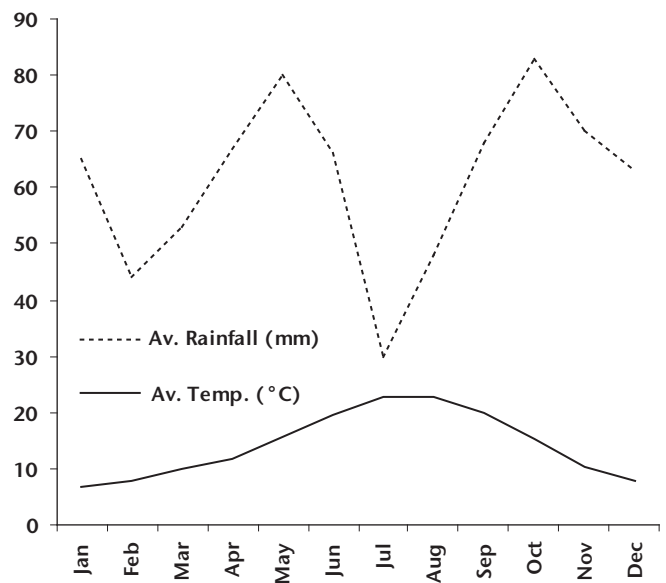
In Uruguay, Mr. Carlos Sebastián MOREY, consultant entomologist for the Governmental Services of Plant Protection, informed us that *P. archon* is very rare in that country, practically unknown, and, needless to say, so far no control measures are recorded against it.

In Argentina there are wide areas with palm trees such as Yatay palm (*Butia yatay*) in the El Palmar National Park, in the Province of Entre Ríos, and Palma Blanca Palm (*Copernicia alba*), in the provinces of Santa Fe, Chaco, Corrientes and Formosa; also, the Campestre palm, *T. campestris*, occurs on the plateau of the central northern part of Argentina, east of Córdoba. Director General of Plant Protection Services, Mr. Carlos A. DEBONA, informed us that, so far, *P. archon* is not considered to be a pest in Argentina. However, he pointed out that, occasionally, some farmers used the organophosphorus contact insecticide Chlorpyrifos against it.

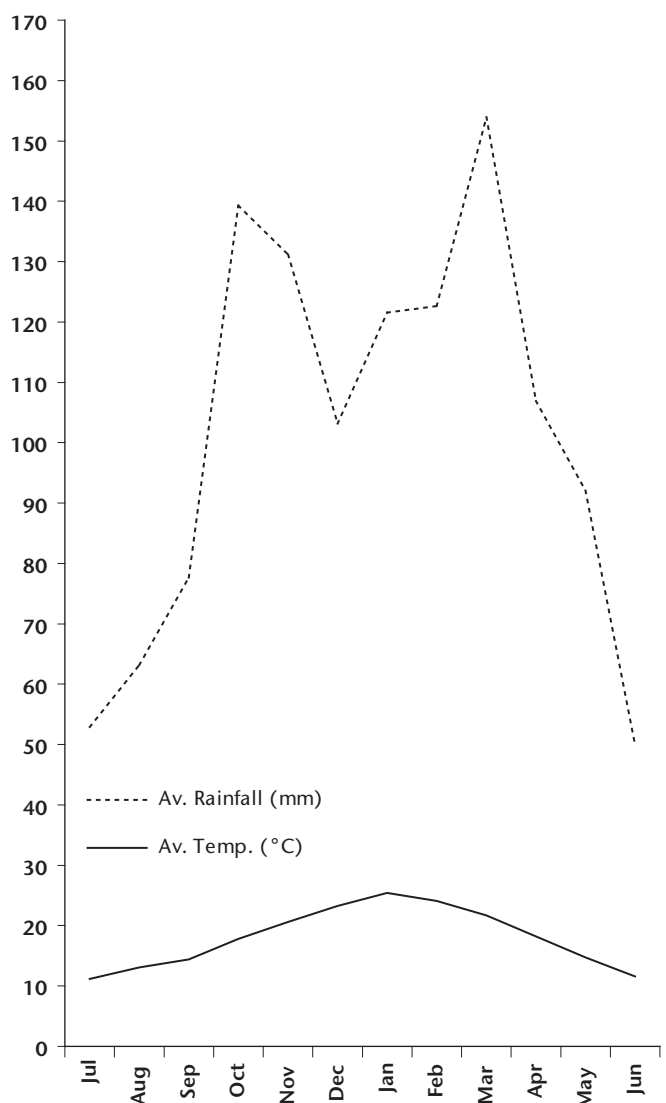
Andrés E. VARGA, Director of the Museo Entomológico Mariposas del Mundo, San Vicente, Buenos Aires, who has considerable experience himself with *P. archon*, confirmed to us that it is not a pest in the Argentinian areas where it is native, since it must be controlled there by natural enemies (see below). However, since the massive introduction, which began around 1998, motivated by aesthetic reasons, of exotic palms (mostly *P. canariensis*, *T. campestris*, *Butia yatay* and *Butia capitata*) in Argentinian areas and cities where palms were not native, mainly in the Province of Buenos Aires, the control of *P. archon* by its natural enemies seemed to have decreased significantly and, there, it has or might become a pest. For instance, at present, in the city of Buenos Aires, many palms are dead or dying because of *P. archon* larvae.

In Europe, where the presence of this moth was first reported in March 2001, in Catalonia, Spain (AGUILAR et al. 2001) and soon thereafter in the Département of Var (France) (SARTO I MONTEYS & AGUILAR 2001, DRESCHER & DUFAY 2001), its pest status is confirmed.

Girona (Catalonia, Spain)



Buenos Aires (Argentina)



Graph 4: Average temperature (in °C) and rainfall (in mm) in the cities of Girona (Catalonia, Spain) and Buenos Aires (Argentina), both in areas where *P. archon* is established.

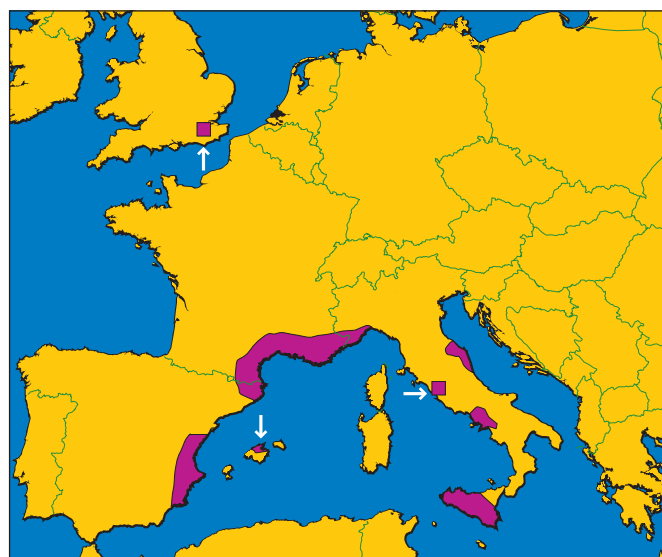
Introduction and spread of *Paysandisia archon* in Europe

Paysandisia archon was most likely introduced, probably independently, into Spain and France (and maybe other European countries) from Argentina, hiding as larvae in imported palm trees, mostly *Butia yatay* (Yatay palm), *T. campestris* (Campestre palm) and *T. fortunei* (Chusan palm).

In Catalonia (Spain), this introduction would have occurred progressively and not long ago, probably starting around 1992–1993, when the first big imports of *T. fortunei* palm trees from Argentina began in this area. One of the main palm nurseries in the province of Girona told us that those imports came from a town placed near Escobar, in the outskirts of the city of Buenos Aires; there, suspicious big holes had been observed on the palm trunks. Until autumn 2000, *P. archon* larvae had passed unnoticed in Catalonia; however, they did not in the Comunidad Valenciana, where they had been found, although not identified, in the second half of the 1990s (see above). Finally, in November 2000, the alarm sprang for the first time at La Cellera de Ter, a small Catalanian town located near the city of Girona, when a local carpenter accidentally found larvae when cutting the palm trunk of a dead *T. fortunei* palm present on his property. Further inspections in the area proved the pest had already spread considerably.

In France, in July 2001, Mr. Jacques DELEUZE, president of “Fous de palmiers”, a French society devoted to palms and part of the International Palm Society, informed Jacqueline Y. MILLER (pers. comm.) that in the last few years many French nurseries imported palms from Argentina (especially *Butia yatay* and *Trithrinax campestris*); some of them containing larvae of *P. archon* resulting in the introduction of this species into southern France. One of the French nurseries located at Hyères, at the Côte d’Azur, Département of Var, seemed to have had infested palms for the last three years, and because those palms were sold to other nurseries, the pest spread. According to Mr. DELEUZE, in a matter of a few days, at Hyères, they discovered hundreds of palms belonging to several species already dead or in very bad condition. These data were partially reported by SARTO I MONTEYS & AGUILAR (2001), DRESCHER & DUFAY (2001, 2002) and REYNAUD et al. (2002)

Once established in Europe, the moth’s spread did not stop, mostly following the commercial routes of palms, either through larvae hiding in palm trunks and leaf rachises or eggs laid on/near the palm crown; also local natural dispersal by adult moths cannot be discarded, as they are powerful flying insects. As to the latter, we found, in a town located more than 10 km from the known Girona strongholds for the castniid, a group of isolated old palms infested by larvae, therefore strongly suggesting the moth had moved there flying because the palms had not been recently bought from infested nurseries. A similar situation was noticed in the Département



Map showing findings of *P. archon* in Europe (updated as of March 2004).

de Var (France), with a distance of 25–30 km (DRESCHER pers. comm.)

In August 2002, one specimen of the moth was discovered in a garden in Bosham, near Chichester, West Sussex, U.K. (PATTON & PERRY 2002), most likely introduced with infested palm trees imported from southern Europe. It was also found in 2002 in several localities belonging to the three provinces of the Spanish Comunidad Valenciana (Castellón de la Plana, Valencia and Alicante) (ANONYMOUS [2003], J. F. BALLESTER-OLMOS pers. comm., J. M. LLORENS pers. comm.), although, as mentioned above, the moth was certainly there at least from 1996–1999. In September 2003, it was detected on the island of Mallorca (Balearic Islands, Spain) (J. J. COLL, pers. comm.), affecting the native Mediterranean Fan palm, *C. humilis*. In France, it also spread to the Départements of Pyrénées-Orientales, Bouches-du-Rhône, Hérault, and Gironde (DRESCHER & JAUBERT 2003). In Italy, ESPINOSA et al. (2003) reported the discovery, in Salerno (Campania), in November 2002, of three adults; DRESCHER & JAUBERT (2003) also quoted it from the Rome area and Sicily, although the presence of this moth in several other areas in Italy (Sanremo, Ventimiglia, Milano and Sicily) had long been suspected (CHAPIN 2002, MÉRIT & MÉRIT 2002); finally, N. ISIDORO (pers. comm.) found a well-established population of *archon* in several nurseries in southern Marche (see above).

A map of Europe is presented summarizing the above data (updated as of March 2004; no recent additions are known presently [March 2005]).

Natural enemies

In Argentina, VARGA (pers. comm.) believes that *P. archon* populations are likely to be controlled by natural enemies such as birds (magpies and other ravens, chalk-browed mockingbird, *Mimus saturninus* (LICHTENSTEIN, 1823) (Mimidae), and others) and ichneumonid wasps

(e.g. species in the genus *Ophion*). However, no factual information exists as yet linking *P. archon* to those supposed natural enemies

In Europe, there are also no factual data as yet concerning *P. archon* natural enemies. One larva found dead in an insectary was found to have nematodes, mites and fly larvae, although most likely these organisms simply colonized the larval body after its death, which is a common occurrence; the same is true for some dead eggs and pupae found invaded by fungi. The nematode was identified as belonging to the genus *Rhabditis*, probably being *Rhabditis (Choriorhabditis) longicaudatus* (BASTIAN, 1865) (C. MONTÓN det.). Also, larvae and puparia of the muscid fly *Phaonia trimaculata* (BOUCHÉ, 1834) (D. VENTURA det.) were found several times within *P. archon* larval galleries in the wild; however this fly is not known to be a parasitoid of lepidopteran larvae (actually its larvae are predacious on other fly larvae), so it was just developing in this particular habitat.

A sample of 168 eggs (hatched or dead) of *P. archon* collected in December 2001 on the fibre webs closest to the crown of two palm species, *C. humilis* and *T. fortunei*, present in commercial palm groves located near Girona (Catalonia, Spain), rendered three eggs which were empty and showed a more or less circular opening very close to the opposite (non-micropylar) pole (Fig. 20). As for the latter, the facts that 1) the egg is empty, 2) the opening is not a split cut along one of the longitudinal ridges but a near-circular hole and 3) the opening appears very close to the opposite pole (the last two facts greatly differing from what is considered to be a normal hatched egg), strongly suggest that those three eggs might have been parasitized by a hymenopterous egg parasitoid; the wasp(s) would have cut open the circular opening when exiting the host egg. Also, the remote possibility that an egg-predacious hemipteran might have been the culprit cannot be ruled out (SARTO I MONTEYS et al. 2005).

On two occasions we observed on the ground wings of *P. archon*, the body fully lacking, therefore suggesting a predacious attack by, most likely, an insectivorous bird or mammal.

Natural enemies have been reported in other Neotropical castniids. In *Castnia eudesmia* GRAY, 1838, MILLER (1986) indicated that, according to a personal communication by L. HERRERA, some unidentified dipterans (most likely Tachinidae) were found associated with the larvae of this Chilean castniid.

In *T. licus*, QUELCH (1910) mentioned that only four unidentified wasp specimens were obtained from among a considerable number of eggs brought to him. MYERS (1932) reported for the first time a tachinid fly as a parasitoid of *T. licus* larvae found in the plant *Heliconia bihai* (Heliconiaceae) in Guyana; this fly, although not identified in MYERS' work, should refer to *Palpozenillia palpalis* (ALDRICH, 1932) (Box 1952). Later, RIBEMBOIN (1964) added the sarcophagid fly *Emdenimyia meyersi* (CURRAN 1938) in sugar cane in Pernambuco (Brazil).

As for predators of *T. licus*, SKINNER (1930) reported that larvae of an elaterid beetle had been found "on one or two occasions" attacking the castniid larvae, although admitting these cases were rare and could not be regarded as a controlling factor. QUELCH (1910) suggested ants as responsible for predation on a considerable number of castniid eggs, an opinion shared by SKINNER. However this latter suggestion was not confirmed by factual data in the wild.

ESQUIVEL (1981, 1983) stated that, in Panamá, predacious ants seemed to be the key factor in the natural control of *T. licus*. He mentioned that the studies carried out showed that sugarcane fields with great numbers of ants had insignificant castniid populations (in some fields, 80–90 % of the eggs and small larvae of the borer were destroyed by predacious ants). He quoted (and figured) six ant species as the more important ones seen visiting the places where the eggs/early larval instars of the borer occurred. Of those, five were identical to those already mentioned from neighbouring Costa Rica by LARA (1965) as natural enemies of *C. atymnius* on banana (see below); the new one being *Solenopsis geminata* (FABRICIUS).

BODKIN (1913) reported that several species of birds, including the "Smooth-billed ani" (*Crotophaga ani* LINNAEUS, 1758, Cuculidae) and the "Great kiskadee" (*Pitangus sulphuratus* (LINNAEUS, 1766), Tyrannidae), were known to prey upon *T. licus* moths in Guyana. SKINNER (1930), in Trinidad, said that certain insectivorous birds, notably the "Kiskidee" (*Pitangus sulphuratus trinitatis* HELLMAYR, 1906) and the "Boat-tailed" or "Carib grackle" (*Quiscalus lugubris* SWAINSON, 1838, Fringillidae), were their principal natural enemies; the "Boat-tailed grackle" was also seen preying on *T. licus* larvae, "when these are turned up in old stools by the forkers during replanting work". QUELCH (1910) suggested rats as being one of the main ground enemies for *T. licus* larvae (the rats would cut open the sugar canes to get the castniid larvae hiding inside). SKINNER (1930) also said that toads and lizards undoubtedly preyed on *T. licus* moths ("particularly on those recently emerged or resting on the moist sides of drains and possibly also on egg-laying ♀♀").

As for pathogens affecting *T. licus*, one fungus, *Cordyceps exasperata* A. F. VITAL 1956 (Clavicipitaceae), was quoted (RIBEMBOIN 1964, BATES 1965) as present in dead or dying larvae of this castniid, although it is not clear if this resulted from a primary or secondary infection. MARQUES et al. (1984) quoted the fungus *Beauveria bassiana* (BALSAMO-CRIVELLI) VUILLEMIN 1912 (Clavicipitaceae), as a natural enemy of *T. licus*, stressing its potential as a biological control agent. ESQUIVEL (1981) noticed larvae and even pupae dying from bacterial or viral disease, showing exactly the same symptoms described earlier by LARA (1965) in larvae of *C. atymnius* (see below).

In *C. atymnius*, LARA (1965) mentioned that ants (Hymenoptera: Formicidae) nesting at the base of the banana suckers make them unsuitable for the castniid ♀♀ to lay their eggs. One ant species, *Pheidole flavens* ROGER, 1863

(Myrmicinae) was actually seen in one instance preying upon a second instar castniid larva located on the inner side of the lowest leaf-sheath of a banana sucker. According to LARA, this fact supports the belief that ants might be of great importance as natural enemies of *C. atymnius*. Besides *P. flavens*, LARA mentioned five more ant species commonly found breeding in the same niches with the castniid eggs and early instar larvae. These were *Ectatomma tuberculatum* (OLIVIER, 1792) "var." *punctigerum* EMERY, 1890 and *Pachycondyla cognata* (EMERY, 1896) (Ponerinae), *Crematogaster* sp. (Myrmicinae), *Azteca* sp. (Dolichoderinae) and *Camponotus atriceps* (SMITH, 1858) ("r." *stercorarius* FOREL, 1885) (Formicinae). However, neither parasitoids nor other predators were observed to occur. In captivity, some larvae appeared to die because of a bacterial or viral disease (cuticle softening and darkening to almost black, internal tissues decomposing and the larvae acquiring a flaccid, watery consistency), although the causal agent was not identified.

In *E. cyparissias*, RUIZ & KORYTKOWSKI (1980) reported and figured a hymenopterous egg parasitoid of the genus *Ooencyrtus* (Encyrtidae), which could not be identified at the species level. The ♀ wasp introduced from 5 to 18 eggs, usually 12, on a single castniid egg; it preferred one or two days old, fertile or infertile, host eggs. Parasitism in the field was found to be about 3 %; in the laboratory was 90–97 %. Mass rearing was tried in the lab and was quite successful. Later, two parasitized castniid eggs, nearing wasp emergence, were placed (per single palm) on green fruit bunches showing a heavy load of castniid eggs, although no results were reported as yet concerning these trials. Also, KORYTKOWSKI & RUIZ (1980) reported they obtained sarcophagid flies (*Oxysarcodexia conclausa* (WALKER, 1861) and *Helicobia* sp.) from prepupal larvae of *E. cyparissias*.

As for predators of *E. cyparissias*, KORYTKOWSKI & RUIZ (1980) reported that many eggs of the castniid (up to 60 %) are preyed upon by different ant species (mostly belonging to the genera *Odontomachus*, *Pheidole* and *Iridomyrmex*) inhabiting the oil palm crown. They also observed three beetle species predating on prepupal larvae of *E. cyparissias*; those were *Carcinops* sp. adults (Histeridae), *Pyrophorus noctilucus* (LINNAEUS, 1758) larvae (Elateridae) and adults of an unidentified Paederini (Staphylinidae). Finally, they saw a falconid bird catching flying *E. cyparissias* moths during daytime.

Symptoms of infestation by *P. archon* on palms

Apart from actually finding remains of several *P. archon* life stages on the palm (hatched/live eggs near/on the crown, cocoons and pupal exuviae located on/protruding from the palm trunk and/or crown (Fig. 21), the latter sometimes also found on the ground), which undoubtedly indicates it has been or it is being infested by the castniid, there are some symptoms seen on palms that might also indicate infestation. These are:

1. presence of sawdust on the palm crown and/or palm trunk (Fig. 22a);
2. presence of perforated or nibbled leaves (non specific) (Fig. 22b);
3. presence of gallery holes (axial and transversal) within the palm trunk (observable when the palm trunk is cut in slices) (Fig. 22c);
4. abnormal development of axillary leaf buds (Fig. 22d);
5. deformation and abnormal twisting of palm trunks (Fig. 22e);
6. abnormal drying up of the palms, specially the core leaves (Fig. 22f). Heavy larval attack may kill the palm tree (Fig. 23).

Some of those symptoms differ a little amongst palm species. For instance, infested palmate-leaved palms, such as *Trachycarpus*, *Chamaerops*, *Washingtonia*, *Trithrinax*, would show, on the fully developed leaf (pierced when young by early instar larvae), a series of consecutive perforations on a circular sector; also, larval galleries will only appear in the palm trunk, not in leaf rachises. On the other hand, pinnate-leaved palms, such as *Phoenix*, would show scattered perforations on the leaves and larval galleries will appear in the palm trunk as well as in leaf rachises.

In the Mediterranean region there are other native lepidopterans attacking graminaceous crops which have been occasionally observed by us boring palm trees (*P. canariensis*, *T. fortunei*), mostly the tender growing point, therefore producing perforations on the leaves similar to those described for *P. archon*. These are the European corn borer, *Ostrinia nubilalis* (HÜBNER, 1796) (Crambidae), and the Mediterranean corn stalk borer, *Sesamia nonagrioides* (LEFÈVRE, 1827) (Noctuidae), both well-known stem-borers of corn (*Zea mays* LINNAEUS, 1753, Poaceae); the damage their larvae produce on palms is generally unimportant unless they attack young palms in nurseries where some might die. The armyworm *Mythimna joannisi* BOURSIN & RUNGS, 1952 (Noctuidae) was quoted by GARRIDO & BALLESTER-OLMOS (1993) boring into two-year old *P. canariensis* and *W. filifera* palms, planted or potted in nurseries located in the provinces of Alicante and Valencia (Comunidad Valenciana, Spain); the larvae bore a central gallery into the palm trunks and fully consumed the growing tops, resulting in death or retarded growth.

Possible measures of control

The biological characteristics of *Paysandisia archon*, as seen above, make its control difficult. The fact that larvae are endophagous for virtually all of their lives (excluding only the very short time elapsed from eclosion to entering the hostplant) makes the use of insecticides much less efficient than when applied on exophagous insects (see below); light traps to collect adult moths cannot be used as they have diurnal habits; poisoned baits to attract

and kill the adult moths would not work as they do not feed in this stage; control by synthetic pheromones (mass-trapping or mating disruption) might be simply not applicable, should the hypothesis of *P. archon* ♀♀ not releasing long-range sex pheromones be confirmed (see above).

In any case, possible measures of control of this castniid could be arranged in four groups:

1. chemical control;
2. mechanical-cultural control;
3. control by synthetic pheromones (subject to the reservation made above);
4. biological control using egg or larval parasitoids, predators on any castniid stage, pathogens such as nematodes, fungi, bacteria and viruses (CHAPIN et al. 2002).

So far, only the first two have been tried against *Paysandisia archon*. As to the chemical control (carried out in the province of Girona, Spain), good results were obtained by wetting the palm crown and palm trunk with contact and/or systemic organophosphorus insecticides (Chlorpyrifos, Acephate and Dimethoate). The only carbamate insecticide used (Aldicarb) was ineffective. Best results were obtained by using Chlorpyrifos 48 %, dose 200 ml/Hl, or Acephate 75 %, dose 150 g/Hl. The experimental design and precise data concerning these trials will be given in a separate paper. Insecticide applications should target first instar larvae before they enter the palm tissues (although it would also work on those which had just entered but are very close to the surface) and be carried out periodically, from late May to late September (in heavily infested plots, once a month; in lightly infested plots or as a preventive measure, only twice: in mid June and in mid August). Those methods did not work satisfactorily when they targeted larvae already hiding inside the palms. It was also noticed that cocoons (on the crown and palm trunk) proved to be impermeable to insecticides, but some adult moths died after contacting freshly applied insecticides. As for the mechanical-cultural control, so far, only pulling-up and burning of the dead or heavily infested palms has been used.

KORYTKOWSKI & RUIZ (1980) and ESQUIVEL (1981) commented on the control methods (used or possible) against *E. cyparissias* in oil-palm and *T. licus* in sugar-cane, respectively. LARA (1966) reported on the cultural control used against *C. atymnius* in banana. Also, biological control was tried against *T. licus* larvae using the fungus *Beauveria bassiana*, either alone (VILAS BOAS et al. 1984) or combined with insecticides (VILAS BOAS et al. 1988), as well as against *E. cyparissias* larvae using entomoparasitic nematodes (imported *Steinernema carpocapsae* (WEISER, 1955) (Mexican strain) and *Heterorhabditis bacteriophora* POINAR, 1976 as well as a native *Heterorhabditis* sp. found in compost in Surinam) (SEGEREN-VAN DEN OEVER et al. 1984). The fungus provided relatively good results in field trials (27.3 % larval mortality if used alone, 45.3 % if associated with the insecticide Monocrotophos); the

nematodes worked relatively well in the lab (within Petri dishes and jars) but were totally ineffective when sprayed on coconut palms (the hostplant for *E. cyparissias* in these trials) despite the fact that the protected environment of the leaf axillae appeared to provide favourable conditions of temperature and humidity.

Acknowledgments

The research that culminated in this paper would have been impossible without the help of many colleagues who contributed in different ways, mostly assisting with literature and useful comments. These are as follows (arranged alphabetically): Dr. Axel O. BACHMANN, Dr. José F. BALLESTER-OLMOS, Dr. Josep BAU, ÉRIC CHAPIN, Joan J. COLL, Elsa DAVICINI, Carlos A. DEBONA, Jean DRESCHER, Dr. Patricia GENTILI-POOLE, Dr. Josep GIRBAL, Susi GÓMEZ, Dr. Jorge M. GONZÁLEZ, Dr. Angel GUERRERO, Martin R. HONEY, Bruno HOSTACHY, Dr. Nunzio ISIDORO, Dr. Gerardo LAMAS, Claudio LITTARDI, José M. LLORENS, Thierry MANIE, Dr. Jacqueline Y. MILLER, Dr. Scott MILLER, Carlos S. MOREY, Nonet PAGÈS, Laia PRIETO, Dr. Carme QUERO and Andrés E. VARGA. Special thanks go to Dr. Richard S. PEIGLER (University of the Incarnate Word, San Antonio, Texas), for his continuous support and editing. Also, we express our gratitude to the Catalanian Department of Agriculture, Service of Plant Protection, in Barcelona and Girona, for financially supporting this research (special mention for Josep R. LLETJÓS, Josep M. VIVES DE QUADRAS, Jaume SERRA and Antoni BOSCH for valuable help in field and paper work). The palm growers Eusebi TORRENT and Domingo RESTUDIS gave us permission to work on their properties and the technical services of Girona's Nurserymen Association (Catalonia), specially Josep M. PAGÈS and Xavier SALVI, helped enormously in arranging and carrying out the trials.

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Received: 13. iv. 2004, 16. viii. 2004